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Origin and early evolution of vertebrate burrowing behaviour

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ABSTRACT

The ability to live underground is widespread among continental vertebrates, so understanding the origin and early evolution of fossorial vertebrates and the architecture and function of the burrows they excavate is an important component of the history of Life on Earth. However, this topic has not been addressed in a synoptic manner; available information is scattered, hampering our understanding of the overall picture. Here, after a short overview of convergent morphological and behavioural adaptations seen in modern fossorial taxa and the diversity of extant vertebrate burrows, we review the fossil record of inferred vertebrate burrows and fossorial vertebrates from the Devonian to the Triassic. Results highlight a probable Devonian earliest occurrence of fossoriality in continental vertebrates (Dipnoi) and a Carboniferous earliest occurrence of fossoriality in tetrapods (Recumbirostra). During the Devonian–Carboniferous, burrows were probably used primarily for aestivation or temporary shelter and evidence of fossoriality is restricted so far to European and North American localities. During the Permian, fossoriality became geographically widespread and developed in new, distantly-related vertebrate lineages, such as diapsids and synapsids. Additionally, there was a size increase and all the main structural features of sub-vertical and sub-horizontal burrows were acquired, as well as the probable use of burrows as permanent shelters or for breeding. We show that the radiation of fossorial forms and increase in abundance and complexity of burrows are contemporaneous with climatic crises such as the Cisuralian aridification, culminating in the Artinskian Warming Event (AWE), and the end-Guadalupian and end-Permian extinction events. After the end-Permian mass extinction, vertebrate fossoriality became a common and widespread feature of continental environments and in more distal floodplain areas, probably as a consequence of changing fluvial regimes. During the Triassic, fossoriality is recorded in even more groups, such as Procolophonidae and Temnospondyli. The first definite complex burrows used as permanent shelters appeared as early as the Early Triassic, and evidence of shared burrow use by different clades appears, suggesting an emerging role of burrowers as ecosystem engineers.

1. Introduction

Among the many adaptations of vertebrates to continental environments, one of the key ecological advances was the ability to live underground, known as fossoriality (e.g., Hildebrand, 1985). Some fossorial animals live permanently underground, and are called subterranean or obligately fossorial (e.g., Hildebrand, 1974). In modern faunas, several distantly related vertebrate groups are known to excavate burrows, as part of diverse behaviours such as aestivation, hibernation, temporary shelter, breeding, and dwelling (e.g., Hildebrand, 1974). Understanding how fossoriality developed during the evolutionary history of vertebrates is therefore crucial to evaluating the evolution of their physiology, behaviour, and interaction with the ecosystem. Moreover, fossorial behaviours in continental or marginal marine environments can be a response to climatic adversities, therefore their study is important to provide a comprehensive picture of

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disrupting climatic events that led to vertebrate extinctions or radiations (e.g., Day et al., 2015). Also, fossil burrows have an important role in the preservation of skeletons and other fossils (e.g., Smith et al., 2021). Nevertheless, the origin and early evolution of burrowing in vertebrates is still poorly understood and constrained (e.g., Benton, 1988) and it is unclear when the main structural features of vertebrate burrows were adopted, as well as how burrow size and complexity varied through time (e.g., Hasiotis et al., 2007; Cardonatto and Melchor, 2018; Melchor and Cardonatto, 2018). Moreover, the acquisition of fossorial features and behaviours consistent with modern-day taxa has not been evaluated comprehensively, stratigraphically, and in evolutionary terms of a phylogenetic framework for early fossorial animals. Finally, no studies have clearly discussed how the development of burrowing is related to climate and palaeogeography at a global scale. The purposes of this study are of different orders: i) Provide a comprehensive reference for the understanding of vertebrate fossoriality based on modern and fossil records, including the study of burrows and skeletons of fossorial animals from an osteological and osteohistological perspective; ii) Review, for the first time, all records of vertebrate fossil burrows and potential burrow-makers in the time interval spanning the Devonian–Triassic to understand the origin and early development of digging behaviour in vertebrates; iii) Identify the major steps in the development of burrow morphological complexity and in the acquisition of fossorial behaviour in different clades; and iv) Review the hypotheses linked to the causes/events that drove the evolution of fossorial/burrowing behaviours and their relationship with vertebrate evolution, such as climate and environmental changes, and palaeobiogeography from the Devonian to the Triassic.

2. Methodology

2.1. Data collection and analysis

Fossoriality in vertebrates is presented first with an overview of present-day burrows and fossorial animals, including burrow structure, behaviour, and macro- and micromorphological adaptations that are key to interpreting fossil burrows and burrowers. A second section presents the study of fossil burrows and burrowers from a taxonomic, taphonomic, and macro- and micromorphological perspective. These sections constitute necessary background information for the main part of the manuscript, which is the review of Devonian-Triassic fossoriality. An extensive literature review has been conducted for both vertebrate burrows and fossorial vertebrates from Devonian-Triassic units. All published occurrences of burrows have been included in Table 1, including the ichnotaxon (when available), location, stratigraphic unit, age, references, key morphological features, key measurements, type of host rock, and possible occurrence of skeletons in the burrow infill. Diameter mean values as well as some key burrow features for each occurrence were plotted with the open source software Python 3.8.5. In this work, the term structural complexity in reference to burrows is intended as the number of morphological features and burrow parts in a burrow system (e.g., Hasiotis et al., 2007). All published occurrences of skeletons that have been interpreted as fossorial because of morphological features and/or their occurrence within a burrow infill have been included in Table 2, including genus/species name, higher level taxonomic grouping, references, location, and age. A description of the occurrences listed in Tables 1–2 has been included in Part 5 (Early vertebrate burrowing record), ordered by type of structure, age, and location. The reported ages are based on an up-to-date stratigraphy of the fossil-bearing units. This database was then discussed as regards burrow structure, burrower phylogeny, burrower bone microstructure, and stratigraphical, palaeobiogeographical, and palaeoecological meanings of fossoriality in relation to vertebrate evolution and palaeoenvironmental/palaeoclimatic change.

2.2. Institutional abbreviations

AMNH = American Museum of Natural History, New York City, New York, USA; BP = Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; CM = Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CMC = Cincinnati Museum Center, Cincinnati, Ohio, USA; FMNH = Field Museum of Natural History, Chicago, Illinois, USA; HU = Halle University, Germany; KUVP = University of Kansas, Lawrence, Kansas, USA; MfNMD = Naturkundemuseum Magdeburg, Germany; MNA = Museum of Northern Arizona, Flagstaff, Arizona, USA; MNG = Stiftung Schloss Friedenstein Gotha, Germany; MNHM = Naturhistorisches Museum Mainz, Germany; NHMUK = The Natural History Museum, London, UK; NMMNH = New Mexico Museum of Natural History & Science, Albuquerque, New Mexico, USA; NMQR = National Museum, Bloemfontein, South Africa; OMNH = Sam Noble Museum, Norman, Oklahoma, USA; SAM = Iziko South African Museum, Cape Town, South Africa; SMNS = Naturkundemuseum Stuttgart, Germany; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; YPM = Yale Peabody Museum, New Haven, Connecticut, USA.

3. Modern-day vertebrate fossoriality

3.1. Vertebrate burrow structures and related behaviours

The key for interpreting burrow ecologies of the past lies in the present. Modern-day vertebrates produce a large variety of burrow morphologies, depending on the producer size, the burrow use, and the sediment they are excavated in (e.g., White, 2005; Cardonatto and Melchor, 2021). Burrows are commonly excavated in loose sediments such as soil, mud, or sand (e.g., Hasiotis et al., 2007). Some animals, notably birds such as the sage grouse, can also dig burrows in the snow (Back et al., 1987). Vertebrates have various reasons for generating or using burrows. Burrows maintain a more constant temperature and humidity throughout the year as compared to the surface, therefore they can be excavated and used to survive seasonal changes across a variety of climatic conditions (e.g., Liow et al., 2009; Riddell et al., 2021). Burrowing animals commonly employ physiological strategies to survive seasonal variation in resource availability, such as aestivation or hibernation. Aestivation, which is a process of lowering the metabolic rate during the hot/dry season, is currently employed mostly by lungfishes (Dipnoi), reptiles, and amphibians (e.g., Storey and Storey, 1990), and is commonly associated with fossoriality. The burrows excavated by these animals to aestivate are generally simple and sub-vertical (e.g., Greenwood, 1986). Some aestivating animals, such as some lungfish, can close the entrance with a plug and then form a cocoon made of mucus to prevent drying (Fig. 1A). Conversely, hibernation is a process involving decreasing body temperature and metabolic rate during the cold season, and is mostly done by mammals (e.g., Nedergaard and Cannon, 1990). The burrows excavated for hibernation can be simple sub-horizontal tunnels with enlarged chambers, such as those excavated and used as dens by bears (González-Bernardo et al., 2020) (Fig. 1B), or complex burrows with several entrances, plugs, branching, and multiple chambers, such as those excavated by marmots (Svendsen, 1976). Another use of certain parts of burrow systems is to drain water. Such function is observed in ground squirrel burrows, which include a hibernation chamber above a specific type of tunnel system thought to be for draining (Shaw, 1926) (Fig. 1C). Spiral burrows, such as those of varanid lizards, are used for breeding, in order to keep sufficient humidity in the nest chamber during the dry season (Doody et al., 2015, 2018). Hatchlings produce their own shaft to reach the surface, which is straight and narrower than the spiral tunnel (Fig. 1D). Other burrows that are also used for breeding include nest chambers in relatively simple burrow systems excavated by one or two animals (e.g., Greenwood, 1986; Doody et al., 2015) or more complex burrow systems excavated by animal communities such as marmots (Svendsen, 1976) (Fig. 1E-F).

Table 1
Devonian-Triassic vertebrate burrows.

Age	Stratigraphic unit	State	Reference	Ichnotaxon	min diameter (cm)	max diameter (cm)	mean diameter (cm)	biconvex bottom ridge	sub-vertical	sub-horizontal	helical	enlarged chamber	tapering	branching	scratch traces	mudstone	sandstone-conglomerate	skeletons
Givetian	Eday Marls	Scotland	Carroll and Trewin, 1995	*Cornulatichnus edayensis*		4	2.0	X	X							X		
Givetian-Fammenian	Old Red Sandstone	Ireland	O'Sullivan et al., 1986		4	8	6.0	X	X								X	
Fammenian	Catskill	Pennsylvania	Woodrow et al., 1973; Friedman and Daeschler, 2006		5	8	6.5	X	X							X		
Serpukhovian	Menard Limestone	Kentucky	Horner and Storrs, 2002; Garcia et al., 2006			10	5.0	X	X							X		cf. *Tranodis*
Pennsylvanian	Breathitt	Kentucky	Thomas and Blodgett, 1986					X	X							X		
Middle Pennsylvanian	Saginaw	Michigan	Carroll, 1965			15	7.5	X	X							X		
Mississippian	Mauch Chunk	Pennsylvania	Storm et al., 2010		15	20	17.5	X		X		X				X	X	
Upper Pennsylvanian	Monongahela	Ohio	Hembree et al., 2011		1	18	9.5	X		X				X		X		
Gzhelian	Ilmenau	Germany	Voigt, 2005			10	5.0	X		X		X			X		X	
Artinskian	Arroyo	Texas	Romer and Olson, 1954		5,5	10	7.8	X	X							X		*Gnathorhiza*
Artinskian	Arroyo	Texas	Dalquest et al., 1989		5,5	25	15.3	X	X							X		*Gnathorhiza*
Artinskian	Vale	Texas	Romer and Olson, 1954		5,5	10	7.8	X	X							X		*Gnathorhiza*
Artinskian	Vale	Texas	Olson and Bolles, 1975		1,5	6	3.8	X	X							X		*Gnathorhiza*
Kungurian	Choza	Texas	Olson and Bolles, 1975					X	X							X		*Brachydectes*
Artinskian	Wellington	Oklahoma	Carlson, 1968		1,5	10	5.8	X	X							X		*Gnathorhiza*
Sakmarian	Speiser Shale	Kansas	McAllister, 1992		1	2	1.5	X	X							X		*Gnathorhiza*
Sakmarian	Speiser Shale	Kansas	Hembree et al., 2004, 2005	*Torridorefugium eskridgensis*	2	7	4.5	X	X				X			X		*Brachydectes*
Sakmarian	Speiser Shale	Kansas	Hembree et al., 2004, 2005	*Torridorefugium eskridgensis*	1,5	3,5	2.5	X	X							X		
Artinskian	Matfield Shale	Kansas	McCahon and Miller, 2015		1	5	3.0	X	X							X		*Gnathorhiza*
Sakmarian-Artinskian	Sangre de Cristo	New Mexico	Vaughn, 1964		4,5	6,5	5.5	X	X			X				X		
Sakmarian-Artinskian	Abo	New Mexico	Berman, 1976		3	10	6.5	X	X							X		*Gnathorhiza bothrotreta*
Artinskian	Robledo Mountains	New Mexico	Voigt et al., 2013			9	4.5	X	X							X		
Cisuralian	Kildare Capes	Prince Edward Island	Langston, 1963		8	10	9.0	X	X							X		

(*continued on next page*)

Table 1 (*continued*)

Age	Stratigraphic unit	State	Reference	Ichnotaxon	min diameter (cm)	max diameter (cm)	mean diameter (cm)	biconvex	bottom ridge	sub-vertical	sub-horizontal	helical	enlarged chamber	tapering	branching	scratch traces	mudstone	sandstone-conglomerate	skeletons
Roadian	Rio do Rasto	Brazil	Francischini et al., 2018		8,2	9,8	9.0	X		X							X		
early Cisuralian	Maroon	Colorado	Voigt et al., 2021			25	12.5	X			X					X		X	
Sakmarian	Tambach	Germany	Martens, 2001a, 2001b, 2005	"*Megatambichnus*"	10	30	20.0	X			X	X	X			X	X	X	
Guadalupian	Teekloof	South Africa	Smith, 1987; Smith et al., 2021	cf. *Daimonelix*	6	16	11.0	X			X	X	X				X	X	*Diictodon*
Guadalupian	Teekloof	South Africa	Smith, 1987; Smith et al., 2021			25	12.5	X			X					X	X	X	*Diictodon*
Lopingian	Naobaogou	China	Liu and Li, 2013		10	25	17.5	X			X					X	X		
Lopingian	Ikakern	Morocco	Lagnaoui et al., 2015			30	15.0	X			X		X		X	X		X	
Lopingian	Dethlingen	Germany	Buchwitz et al., 2018		13	28	20.5	X	X		X					X		X	
Lopingian-Early Triassic	Buena Vista	Brazil	Francischini et al., 2023		6	17,2	11.6	X	X		X	X				X		X	
Early Triassic	Katberg	South Africa	Bordy and Krummeck, 2016		3,5	6	4.8	X		X							X		
Early-Middle Triassic	Fedorovkian-Donguzian units	Russia	Sennikov, 2018		5	10	7.5	X		X								X	
Late Triassic	Chinle	Utah, Arizona, Colorado, New Mexico	Dubiel et al., 1987		2	11	6.5	X		X							X		
Late Triassic	Chinle	New Mexico	Lucas et al., 2010	*Redondarefugium abercrombieorum*	4,8	7,2	6.0	X		X			X					X	
Early Triassic	Palingkloof	South Africa	Damiani et al., 2003	cf. *Reniformichnus* isp.		20	10.0		X		X					X	X		*Thrinaxodon liorhinus*
Early Triassic	Palingkloof	South Africa	Modesto and Botha-Brink, 2010		12	34	23.0	X			X						X		*Lystrosaurus*
Early Triassic	Palingkloof	South Africa	Botha-Brink, 2017		17	30	23.5	X			X					X	X		*Lystrosaurus curvatus*
Early Triassic	Normandien	South Africa	Fernandez et al., 2013		9,6	15	12.3				X						X		*Thrinaxodon liorhinus*, *Broomistega putterilli*
Early Triassic	Katberg	South Africa	Bordy et al., 2009, 2011		25	40	32.5	X			X					X	X		
Early Triassic	Katberg	South Africa	Krummeck and Bordy, 2018	*Reniformichnus katikatii*	5	14,7	9.9		X		X					X	X		
Early Triassic	Palingkloof, Katberg	South Africa	Groenewald, 1991	cf. *Reniformichnus* isp.	20	50	35.0	X			X					X	X		cf. *Lystrosaurus*
Early Triassic	Palingkloof, Katberg	South Africa	Groenewald, 1991		20	50	35.0	X			X		X			X	X		*Lystrosaurus* sp., *Dicynodon lacerticeps*

(*continued on next page*)

Table 1 (*continued*)

Age	Stratigraphic unit	State	Reference	Ichnotaxon	min diameter (cm)	max diameter (cm)	mean diameter (cm)	biconvex	bottom ridge	sub-vertical	sub-horizontal	helical	enlarged chamber	tapering	branching	scratch traces	mudstone	sandstone-conglomerate	skeletons
Early Triassic	Palingkloof, Katberg	South Africa	Groenewald, 1991		20	50	35.0	X			X			X			X		cf. *Lystrosaurus*
Early Triassic	Palingkloof, Katberg	South Africa	Groenewald, 1991		3	15	9.0	X			X				X		X		cf. *Procolophon*
Early Triassic	Fremouw	Antarctica	Miller et al., 2001	*Reniformichnus* isp.	8	19	13.5		X		X	X			X	X	X		
Early Triassic	Fremouw	Antarctica	Miller et al., 2001		2	7	4.5	X			X				X	X	X		
Early Triassic	Fremouw	Antarctica	Sidor et al., 2008	*Reniformichnus* isp.	8,5	15,7	12.1		X		X					X	X		
Early Triassic	Dooralong Shale	Australia	McLoughlin et al., 2020	*Reniformichnus australis*	1	15	8.0		X		X					X	X		
Early Triassic	Burgersdorp (former Driekoppen)	South Africa	Groenewald et al., 2001		1,1	15,4	8.3		X		X			X	X	X	X		*Trirachodon*
Middle Triassic	Burgersdorp	South Africa	Shone, 1978, Bordy et al., 2019		15	23	19.0		X		X				X	X		X	
Middle Triassic	Burgersdorp	South Africa	Sidor et al., 2008		3	5	4.0		X		X					X	X		
Middle Triassic	Burgersdorp	South Africa	Wolvaardt, 2021	*Reniformichnus katikatii*	6	8	7.0	X	X		X				X	X	X		
Middle Triassic	Burgersdorp	South Africa	Wolvaardt, 2021		8	14,5	11.3	X	X		X		X		X	X	X		
Middle Triassic	Burgersdorp	South Africa	Wolvaardt, 2021					X			X					X	X		*Microgomphodon*
Middle Triassic	Lashly	Antarctica	Sidor et al., 2008		3	5	4.0		X		X				X	X	X		
Middle Triassic	Timezgadiouine	Morocco	Voigt et al., 2011		6	20	13.0	X			X		X		X	X		X	
Middle Triassic	Otter Sandstone	England	Gallois, 2013		10	30	20.0	X			X		X					X	
Middle Triassic	Buntsandstein	France	Ellenberger, 1976	*Cynodontipus polythrix*	5	5	5.0		X		X		X			X		X	
Middle Triassic	Buntsandstein-Muschelkalk	Germany	Ellenberger, 1976	*Cynodontipus polythrix*	5	5	5.0		X		X					X	X		
Middle Triassic	Tarjados	Argentina	Krapovickas et al., 2013		8	20	14.0		X		X		X					X	
Late Triassic	Blomidon	Nova Scotia	Sues and Olsen, 2015	cf. *Cynodontipus* isp.	5	10	7.5		X		X					X		X	
Late Triassic	Chañares	Argentina	Fiorelli et al., 2018		10	25	17.5		X		X			X	X	X		X	
Late Triassic	Ischigualasto	Argentina	Colombi et al., 2008, 2012		10	15	12.5	X			X		X		X		X	X	
Late Triassic	Los Colorados	Argentina	Colombi et al., 2012		20	50	35.0	X			X				X		X		
Late Triassic	Keuper	Poland	Tałanda et al., 2011		7	9	8.0				X		X				X		
Late Triassic	Chinle	Arizona	Hasiotis et al., 2004		4	15	9.5	X			X	X	X		X		X		

Table 2
Carboniferous-Triassic vertebrate burrowers.

Taxon	Group	Publication	State	Time interval
cf. *Tranodis*	Dipnoan	Garcia et al., 2006	Kentucky	Mississippian
Gnathorhiza	Dipnoan	Carlson, 1968	Oklahoma, Texas	Cisuralian
Diabloroter bolti	Recumbirostran	Mann and Maddin, 2019	Illinois	Pennsylvanian
Infernovenator steenae	Recumbirostran	Mann et al., 2019	Illinois	Pennsylvanian
Joermungandr bolti	Recumbirostran	Mann et al., 2021	Illinois	Pennsylvanian
Nagini mazonense	Recumbirostran	Mann et al., 2022	Illinois	Pennsylvanian
"*Lysorophus*"	Recumbirostran	Bolt and Wassersug, 1975	Illinois, Pennsylvania, W Virginia, New Mexico, Kansas, Maryland, Oklahoma, Texas, Ohio	Pennsylvanian-Cisuralian
Brachydectes newberryi	Recumbirostran	Bolt and Wassersug, 1975	illinois, Ohio, W Virginia, Nebraska	Pennsylvanian-Cisuralian
Huskerpeton englehorni	Recumbirostran	Huttenlocker et al., 2013	Nebraska	Cisuralian
Quasicaecilia texana	Recumbirostran	Pardo et al., 2015	Texas	Cisuralian
Carrolla craddocki	Recumbirostran	Maddin et al., 2011	Texas	Cisuralian
Nannaroter mckinziei	Recumbirostran	Anderson et al., 2009	Oklahoma	Cisuralian
Rhynchonkos stovalli	Recumbirostran	Szostakiwskyj et al., 2015	Oklahoma	Cisuralian
Aletrimyti gaskillae	Recumbirostran	Szostakiwskyj et al., 2015	Oklahoma	Cisuralian
Dvellecanus carrolli	Recumbirostran	Szostakiwskyj et al., 2015	Oklahoma	Cisuralian
Llistrofus pricei	Recumbirostran	Gee et al., 2019	Oklahoma	Cisuralian
Proxilodon bonneri	Recumbirostran	Huttenlocker et al., 2013	Kansas	Cisuralian
Tambaroter carrolli	Recumbirostran	Henrici et al., 2011	Germany	Cisuralian
Batropetes	Recumbirostran	Glienke, 2015	Germany	Cisuralian
Eunotosaurus africanus	Diapsid	Lyson et al., 2016	South Africa	Guadalupian
Pappochelys rosinae	Diapsid	Schoch et al., 2019	Germany	Middle Triassic
Procolophon trigoniceps	Procolophonid	Botha-Brink and Smith, 2012	South Africa, Antarctica, Brazil	Early Triassic
Sauropareion anoplus	Procolophonid	Botha-Brink and Smith, 2012	South Africa	Early Triassic
Teratophon spinigenis	Procolophonid	Botha-Brink and Smith, 2012	South Africa	Early Triassic
Diictodon feliceps	Dicynodont	Smith, 1987	South Africa	Guadalupian
Cistecephalus microhinus	Dicynodont	Cox, 1972	South Africa	Lopingian
Cistecephaloides boonstrai	Dicynodont	Cluver, 1974	South Africa	Lopingian
Kawingasaurus fossilis	Dicynodont	Cox, 1972	Tanzania	Lopingian
Sauroscaptor tharavati	Dicynodont	Kammerer et al., 2016	India	Lopingian
Kembawacela kitchingi	Dicynodont	Angielczyk et al., 2019	Zambia	Lopingian
Oudenodon	Dicynodont	Botha, 2003	South Africa, Zambia, Malawi	Lopingian
Lystrosaurus curvatus	Dicynodont	Botha-Brink, 2017	South Africa, Antarctica	Lopingian-Early Triassic
Tetracynodon darti	Therocephalian	Fontanarrosa et al., 2019	South Africa	Lopingian-Early Triassic
Bauria cynops	Therocephalian	Groenewald et al., 2001	South Africa	Early-Middle Triassic
Microgomphodon oligocynus	Therocephalian	Wolvaardt, 2021	South Africa	Early-Middle Triassic
Procynosuchus delaharpeae	Cynodont	Kümmell, 2009	Germany, Russia, South Africa, Tanzania, South Africa	Lopingian-Early Triassic
Galesaurus planiceps	Cynodont	Butler et al., 2018	South Africa	Early Triassic
Thrinaxodon liorhinus	Cynodont	Damiani et al., 2003	South Africa, Antarctica	Early Triassic
Trirachodon	Cynodont	Botha and Chinsamy, 2004	South Africa, Namibia, Zambia	Early-Middle Triassic
Langbergia modisei	Cynodont	Groenewald et al., 2001	South Africa	Early-Middle Triassic
Andescynodon mendozensis	Cynodont	Chinsamy and Abdala, 2008	Argentina	Middle Triassic
Massetognathus pascuali	Cynodont	Garcia Marsà et al., 2022	Argentina	Late Triassic
Probainognathus jenseni	Cynodont	Garcia Marsà et al., 2022	Argentina	Late Triassic
Chinlestegophis jenkinsi	Temnospondyl	Pardo et al., 2017	Colorado	Late Triassic
Funcusvermis gilmorei	Temnospondyl	Kligman et al., 2023	Colorado	Late Triassic

Complex burrows can be used permanently throughout the year; in this case they are considered dwelling structures (e.g., Šumbera et al., 2008). Other burrow uses include escaping from predators, for which multiple entrances and/or bolt tunnels can be excavated, usually as parts of complex burrows. Bolt tunnels, such as those excavated by African mole rats (Bathyergidae), are inclined tunnels that go deep into the ground (Lovegrove and Painting, 1987) (Fig. 1G). Burrows, and especially complex burrows, can be used for finding or storing food, such as for the African mole rats that excavate either spiral tunnels around tubers (Fig. 1G) or lateral branching tunnels to forage tubers (Lovegrove and Painting, 1987). Foraging burrows can also be used for hunting, as in some owls (Thompson and Anderson, 1988). Another use of burrows, more commonly in complex burrows, is the disposal of garbage or fecal material, observed for instance in marmots and mole rats (Svendsen, 1976; Herbst and Bennett, 2006). Finally, a given burrow can be used by different species (the burrow maker and non-excavating taxa), thus creating new ecological niches for the non-burrower species and so constituting an important feature of the entire local ecosystem. For instance, research has shown that complex burrows excavated by porcupines can also be inhabited by jackals, bats, and snakes (Mukherjee et al., 2017). Burrow systems including several spiral tunnels excavated by varanids have been shown to contain up to 28 species of vertebrates (Doody et al., 2021). Gopher tortoises (*Gopherus polyphemus*) have been proposed to be keystone species because their burrows increase the local biodiversity (Catano and Stout, 2015). In these cases, the producers are considered ecosystem engineers because the burrows that they build host and support complex ecosystems.

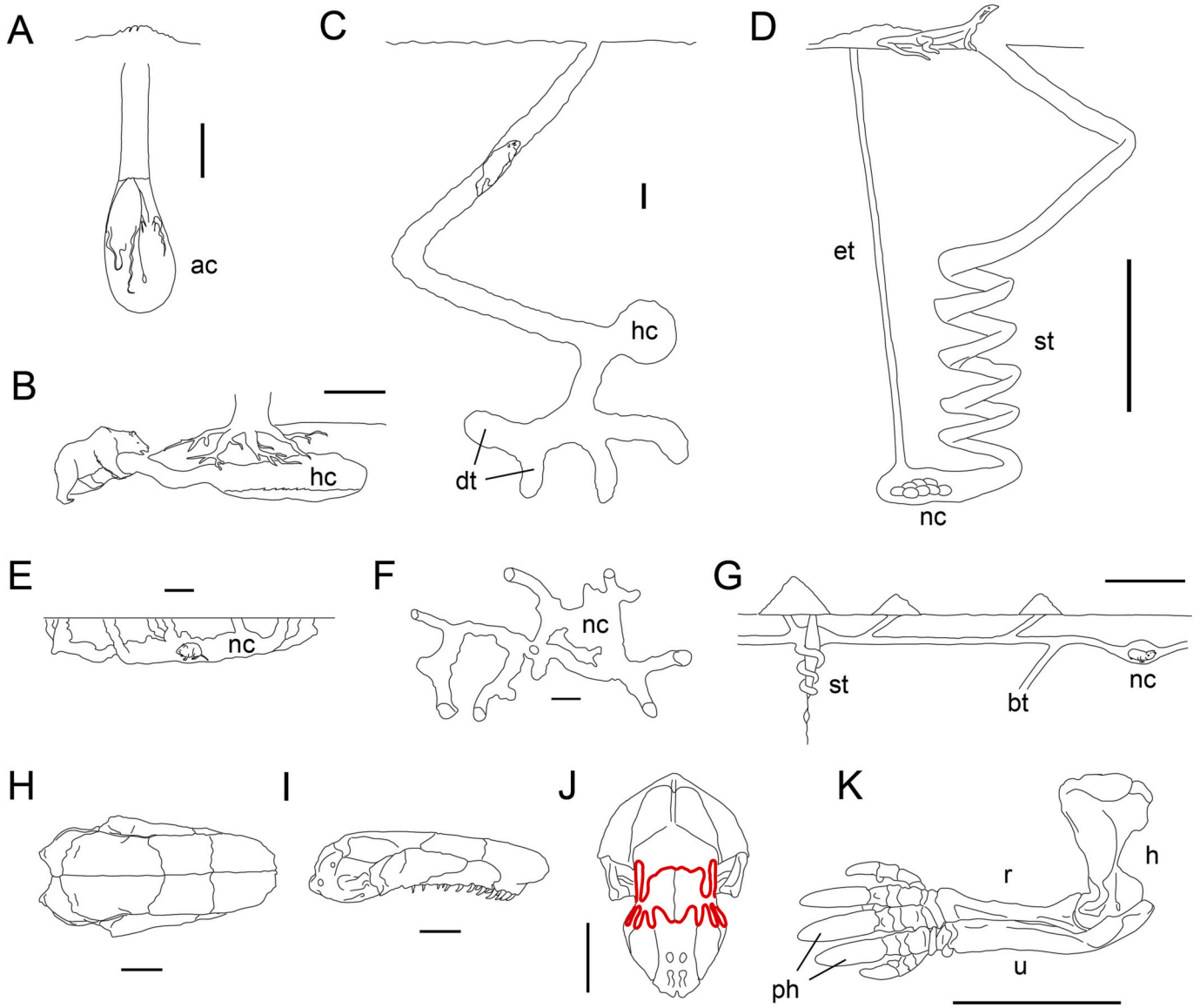

Fig. 1. Modern-day burrows (A-G) and fossorial adaptations (H—K). A) Aestivation burrow of the African lungfish *Protopterus annectens*. Lateral view. ac = aestivation chamber. Scale bar = 10 cm. Re-drawn from Greenwood (1986). B) Excavated den of the brown bear, *Ursus arctos*, lateral view. hc = hibernation chamber. Scale bar = 1 m. Re-drawn from Kumar et al. (2017) and González-Bernardo et al. (2020). C) Hibernation burrow of the Columbian ground squirrel, *Urocitellus columbianus*, lateral view. dt = draining tunnels. Scale bar = 10 cm. Re-drawn from Shaw (1926). D) Nest burrow of the monitor lizard *Varanus gouldii*, lateral view. nc = nest chamber, sp. = spiral tunnel, et = escape tunnel. Scale bar = 1 m. Re-drawn from Doody et al. (2018). *E*-F) Communal complex burrow of the prairie vole, *Microtus ochrogaster*. Scale bars = 10 cm. Redrawn from Mankin and Getz (1994) and Tripp et al. (2021). E) Lateral view. F) Top view. G) Burrow of the Damara molerat, *Cryptomys damarensis*, lateral view. bt = bolt tunnel. Scale bar = 1 m. Re-drawn from Lovegrove and Painting (1987) and Zöttl et al. (2022). H—I) Skull of the caecilian *Boulengerula spawlsi*. Scale bar = 1 cm. Re-drawn from Wilkinson et al. (2017). H) Dorsal view. I) Lateral view. J) Skull of the amphisbaenid *Agamodon anguliceps*, front view. Interdigitated suture lines in red. Scale bar = 2 mm. Re-drawn from Gans (1960). K) Right forearm of the echidna, *Tachyglossus aculeatus*, dorsolateral view. h = humerus, r = radius, u = ulna, ph = phalanges. Scale bar = 5 cm. Re-drawn from Hildebrand (1974). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Vertebrate digging techniques

Burrowing is a common behaviour in modern-day vertebrates, with representation across a variety of distantly-related taxa, such as fishes, amphibians, mammals, reptiles, and birds (Hildebrand, 1974). Fossorial and especially subterranean animals acquired convergent morphological adaptations, mostly based on the underground physical conditions and on their digging technique (Shimer, 1903; Hildebrand, 1985; Vassallo et al., 2021). Underground conditions generally imply lack of light, low oxygen levels, limited space, high pressure of the sediment on the body, high humidity, and stable temperature. Furthermore, digging implies moving large quantities of sediment, which can result in filling the mouth of the digger with indigestible material (e.g., Sherratt et al., 2014).

When it comes to digging techniques, many vertebrates use their head, or more specifically their mouth and teeth, to dig. Lungfishes use the mouth to bite the sediment and expel it through branchial openings (Greenwood, 1986). Several rodents use their large incisors in what is called chisel-tooth digging (Hildebrand, 1974; Gomes Rodrigues et al., 2011; Becerra et al., 2012), with some (e.g., *Rhizomys*, *Spalacopus*) relying almost solely on the incisors for digging. Worm lizards (Amphisbaenia) use their head to compact the sediment and open the burrow with dorsal and ventral movements; this is called head-first digging (e.g., Catena and Hembree, 2014; Hohl et al., 2014, 2017;

Hipsley et al., 2016; Bergmann and Berry, 2021), also known as head-lift digging or soil-crawling, the latter particularly referring to animals with an elongated body and reduced limbs (Hildebrand, 1974, 1985).

Forelimbs are employed in digging by many groups of fossorial animals. Forelimb digging methods include: scratch-digging, humeral-rotation digging, and hook-and-pull digging (Hildebrand, 1974, 1985; Nakai and Fujiwara, 2023). Scratch-digging, used for instance by ground squirrels and mole rats, involves the pronation/supination movement of the forelimb, which cuts the sediment with claws and then moves it backwards (Hildebrand, 1985; Montoya-Sanhueza et al., 2022). Humeral-rotation digging, or rotational-thrust digging, such as that used by moles (Talpidae), involves the rotation of the humerus to move their shovel-like hands, while the elbow does not bend significantly (Hildebrand, 1974, 1985; Gobetz, 2005; Costes et al., 2023). Hook-and-pull digging, used by anteaters (Vermilingua), consists of moving the forelimb to grab the sediment and then pulling it back (Taylor, 1978; Hildebrand, 1985; Lyra da Silva et al., 2023). Finally, some animals, such as frogs, primarily use their hindlimbs to dig, a specialization called hind feet-first digging (e.g., Emerson, 1976; Hildebrand, 1985; Blotto et al., 2022). Hindlimbs are also commonly used to dispose of excavated sediment by a variety of types of digging animals (e.g., Hildebrand, 1974, 1985). Furthermore, several vertebrates use more than one technique to dig. For instance, pocket gophers (Geomyidae) or mole rats employ a combination of chisel-tooth and scratch-digging (Hildebrand, 1985; Montoya-Sanhueza et al., 2022), while armadillos combine scratch-digging with head-first digging (Clerici et al., 2018; Cardonatto and Melchor, 2023). The various digging techniques also reflect the skeletal morphological and microstructural adaptations of these taxa.

3.3. Morphological correlates to fossoriality in vertebrates

In fossorial animals, adaptations for burrowing can be found throughout the entire skeleton and soft tissues. Examples of soft tissue adaptations include: the short, soft hairs of moles, which can brush in any direction to minimize abrasion on burrow walls (Hildebrand, 1974); sensory organs such as whiskers or Eimer's organ of the star-nosed mole (*Condylura cristata*) (Eimer, 1871); protective skin layers covering the eyes of many fossorial animals such as caecilians, amphisbaenians, marsupial moles (Notoryctidae), true moles (Talpidae), or golden moles (Chrysochloridae) (Hildebrand, 1974); and modifications of digging tools to improve the movement of soil, seen for example in the webbed feet of toads or golden moles (Hildebrand, 1974).

3.3.1. Cranial adaptations

The general functions of cranial adaptations in burrowing vertebrates are: i) reinforcement and support of the skull; ii) preventing dirt from entering the sensory organs or the mouth; and iii) functioning as a primary or secondary digging tool. These adaptations are most pronounced in vertebrates that utilize their skull as the primary digging tool, however, even those that primarily use their limbs often exhibit some cranial adaptations for fossoriality. The skull of fossorial tetrapods is commonly spade-shaped, and projections such as horns are reduced, so as not to interfere with movement through a dense substrate (Shimer, 1903).

Adaptations that reinforce and support the skull include the modification of neurocranial elements into larger compound units, to better withstand compressive forces, observed in many groups of fossorial tetrapods such as snakes (Olori and Bell, 2012), amphisbaenians (Gans, 1960), and caecilians (Wake, 2003) (Fig. 1H-I). Highly interdigitated sutures in the skulls of fossorial animals are another feature that is often identified, notably in amphisbaenians (Gans, 1960, 1973) (Fig. 1J), as well as a closed or fused temporal region (Nussbaum, 1983; Sherratt et al., 2014) (Fig. 1I), further strengthening the skull.

In many tetrapods, the skull is actively involved in burrowing. In head-lift digging, animals such as frogs, moles, rodents, or caecilians utilize the top of their broad, and often short, spatulate shaped skulls to move and compact soil (Hildebrand, 1985). Common cranial adaptations for head-lift digging include a broad occipital region (Fig. 1J) and a prominent nuchal crest, which provides a large attachment area for the neck musculature (Hildebrand, 1985). Chisel-tooth diggers utilize their large, forward-projecting incisors as digging tools.

Furthermore, many adaptations in the skull prevent dirt from entering the mouth or sense organs (Hildebrand, 1974). External ears and eyes tend to be small and can be completely reduced, especially in animals that exhibit subterranean lifestyles and live mostly in low light conditions. For example, in the mole *Talpa*, external ears are absent and eyes are reduced to vestigial dots (Shimer, 1903). Fossorial animals tend to have a close registration of jaws to prevent dirt from entering the mouth. The large incisors of chisel-tooth diggers, such as Bathyergidae, can also prevent this by extending over the lips (Shimer, 1903). The subterminal position of the mouth occurring in many highly fossorial caecilians (e.g., Sherratt et al., 2014) may also help prevent soil from entering the mouth during head-first burrowing.

3.3.2. Postcranial adaptations

Postcranial adaptations span throughout the axial skeleton, the pectoral and pelvic girdles, and the limbs. Most postcranial adaptations improve the output force of the digging tools, by providing increased muscle attachment areas or enhanced lever-systems, to allow animals to move through a dense substrate such as soil. Furthermore, adaptations may increase overall skeletal robustness or provide tools for loosening and moving soil (e.g., Hildebrand, 1985).

Many fossorial vertebrates use their limbs for digging. As a result, their limbs exhibit a variety of modifications to facilitate burrowing underground. The limbs of these taxa tend to be short and stout with broad, shovel-shaped autopodia (Shimer, 1903). In most burrowing tetrapods, the majority of fossorial adaptations are observed in the forelimbs, as these are responsible for most of the digging. Contra this usual pattern, many frogs dig with their hind-feet, and therefore evolved strong, robust hindlegs with tarsal tubercles on their webbed feet to loosen the soil (Emerson, 1976). Forward burrowing tetrapods generally have well-developed pectoral girdle elements that provide large muscle attachments to power the strong forelimbs. Many burrowing animals possess large acromion processes on their scapulae, such as golden moles, aardvarks, armadillos, and gopher tortoises (Hildebrand, 1985; Lyson et al., 2016). In these taxa, the forelimb bones provide large areas for muscle insertion and broad joint articulations. The humerus has a short, thick diaphysis, broad epicondyles, and a distinct deltopectoral crest for muscle insertions. The radius is short and broad. The ulna possesses an elongated olecranon process that acts as the lever arm for the elbow flexors. In golden moles, the olecranon process can make up more than half of the ulna length (Hildebrand, 1985). All of the forelimb adaptations mentioned above can also be observed in the echidna (*Tachyglossus*), a fossorial monotreme (Fig. 1K). Numerous fossorial tetrapods also make use of their claws for digging, and as a result many have modifications to their unguals and associated phalanges. Generally, proximal phalanges are short and thick and unguals are long and broad (Hildebrand, 1974), as seen in the manus of *Tachyglossus* (Fig. 1K). The claws of many scratch-digging mammals that use them to penetrate hard substrates (e.g., rodents, armadillos, golden moles) are laterally compressed and fast-growing (Gambarian, 1960; Hildebrand, 1985). Loss and fusion of bones can further increase rigidity. This is frequently expressed in the reduction of the phalangeal formula and fusion of proximal elements to the metacarpals (e.g., gopher tortoise, golden moles, marsupial moles) (Hildebrand, 1985).

The axial skeleton of fossors is usually modified to endure the forces exerted by digging. The cervical, lumbar, and sacral vertebrae in particular must withstand high compressive forces. Hence, fusion of those vertebrae can be observed in some fossorial mammals, such as marsupial moles and armadillos (Shimer, 1903). The neck region is commonly short, consisting of short and wide, sturdy cervical vertebrae with massive zygapophyses and bulbous neural spines that provide

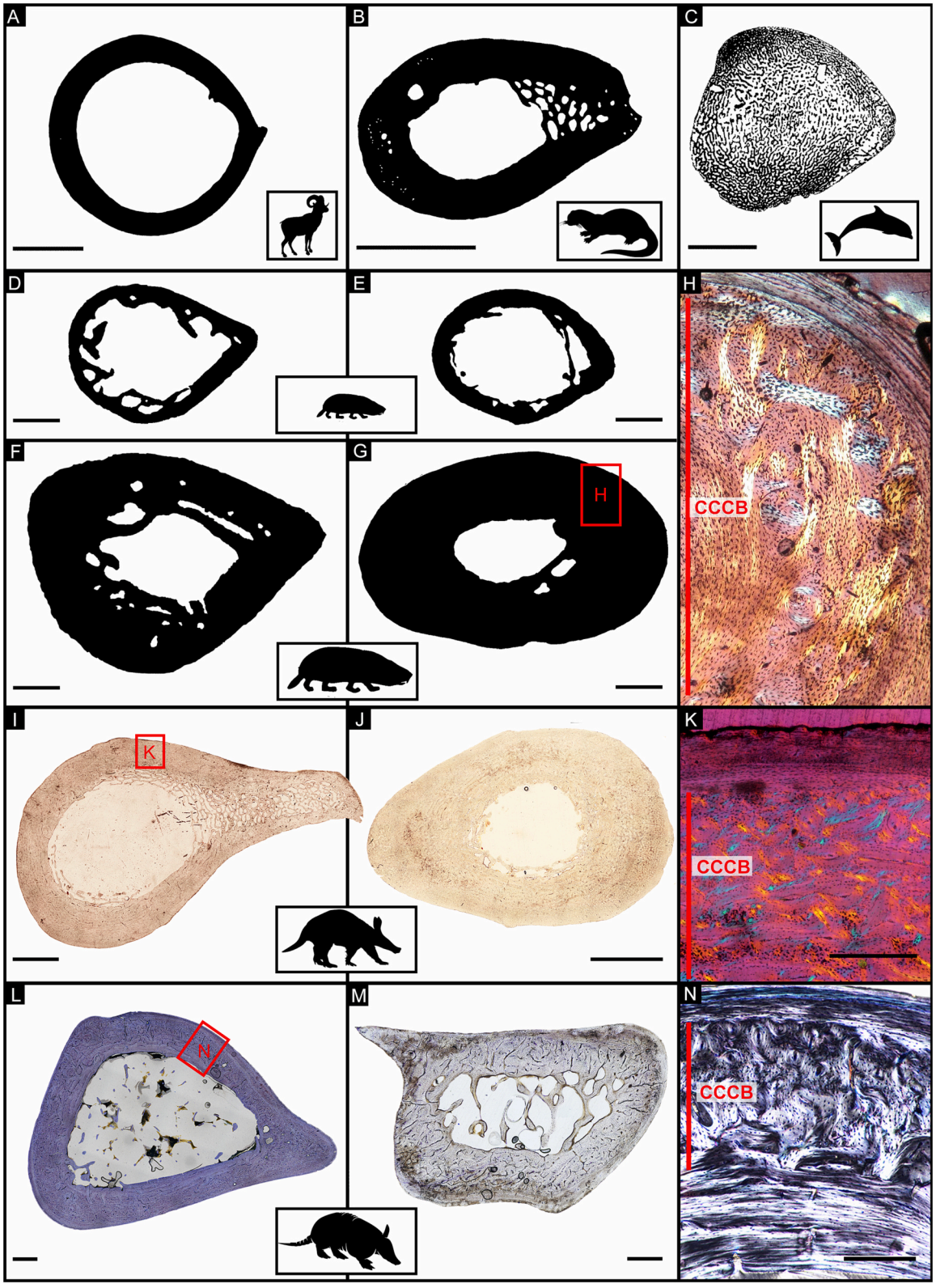

Fig. 2. Mid-diaphyseal limb bone microstructure in selected terrestrial (A), semi-aquatic (B), pelagic (C), and fossorial (D—N) extant mammals. All specimens represent adult individuals, except D and E. A) Femur of *Ovis ammon.* B) Humerus of *Lutra lutra.* C) Humerus of *Delphinus delphis.* D) Humerus of a juvenile *Bathyergus suillus.* E) Femur of a juvenile *Bathyergus suillus.* F) Humerus of an adult *Bathyergus suillus.* G) Femur of an adult *Bathyergus suillus.* H) Close up on the cortex of *Bathyergus suillus* femur formed of large amounts of compacted coarse cancellous bone (CCCB; in polarized light with lambda filter). I) Femur of *Orycteropus afer.* J) Tibia of *Orycteropus afer.* K) Close up on the cortex of *Orycteropus afer* femur formed of large amounts of compacted coarse cancellous bone (in polarized light with lambda filter). L) Femur of *Dasypus novemcinctus.* M) Tibiofibula of *Dasypus novemcinctus.* N) Close up on the cortex of *Dasypus novemcinctus* femur formed of large amounts of compacted coarse cancellous bone (in polarized light). Scale bars equal 1 mm in D-G, L, M; 5 mm in A, B, I, J; 10 mm in C; 0.5 mm in K, N. Images D to H were provided by G. Montoya-Sanhueza; I to K by J. Botha and L. Legendre; L to N by C. Heck.

attachment sites for the strong neck musculature used in head-lift digging, as in the gopher tortoise (Bramble, 1982; Lyson et al., 2016). In fossorial mammals, the sacral complex often includes a larger number of vertebrae (up to 13 in armadillos), either by fusion or suturing of caudal vertebrae (Hildebrand, 1985). In gopher tortoises and giant anteaters, the ribs are broadened for greater muscle attachment and to provide a strong base for the limb apparatus (Jenkins Jr., 1970; Lyson et al., 2016). This contributes to an overall fusiform or spindle-like body shape commonly seen in fossorial mammals such as moles. A different body type is found in soil crawling animals that primarily use their head to burrow. Here, the axial skeleton is greatly elongated by increasing the number of vertebrae, and limbs often become obsolete for propulsion, hence they are reduced in many tetrapod lineages, such as snakes, amphisbaenians, and caecilians (Hildebrand, 1974).

3.4. Osteohistological observations in fossorial tetrapods

Comparative studies across extant tetrapods have demonstrated that an ecological and biomechanical signal is recorded throughout the life of an organism in the internal structure of its long bones and vertebrae (e.g., Nopcsa, 1923; Currey and Alexander, 1985; Canoville and Laurin, 2010; Dumont et al., 2013; Houssaye et al., 2014; Amson and Bibi, 2021; Gônet et al., 2023a). Taxa with similar lifestyles (e.g., terrestrial, aerial, semi-aquatic, aquatic) thus show convergent microanatomical adaptations (see Canoville et al., 2021 and references therein for an overview). For instance, terrestrial tetrapods tend to have tubular long bones with compact cortices and an open medullary cavity (Fig. 2A). Semi-aquatic (e.g., crocodilians, hippopotamus, pinnipeds) or fully aquatic taxa inhabiting shallow waters and coastal environments (e.g., sirenians) exhibit thicker bone cortices (i.e., pachy-osteosclerotic condition) with a medullary cavity that can be invaded by trabeculae (Fig. 2B). By contrast, pelagic, fast swimming species (e.g., extant whales and marine turtles) show rather spongious (i.e., osteoporotic-like) limb elements resulting in a bone mass decrease as compared to their terrestrial relatives (Fig. 2C). Following the *actualism* principle and when used in a standardized and comparative phylogenetic framework, bone microanatomy can thus be used to reconstruct the palaeoecology of long-extinct animals whose locomotion and lifestyle are poorly documented by external morphology and taphonomy (e.g., Germain and Laurin, 2005; Thewissen et al., 2007; Canoville and Laurin, 2010; Canoville and Chinsamy, 2015; Houssaye et al., 2015; Gônet et al., 2023a, 2023b).

Recently, researchers started investigating more specifically the vertebral and long bone microstructural adaptations to sustained digging activity and life underground. Except for a few notable studies on extant reptiles (Houssaye et al., 2010; Gônet et al., 2023a, 2023c), most of these works focused primarily on fossorial adaptations across mammals (e.g., Amson, 2021; Amson and Bibi, 2021; Amson et al., 2022; Gônet et al., 2023b) or specific mammalian groups such as mustelids (Amson and Kilbourne, 2019; Kilbourne and Hutchinson, 2019; Parsi--Pour and Kilbourne, 2020), xenarthrans (Straehl et al., 2013; Amson et al., 2017; Heck et al., 2019; Zack et al., 2023), talpids (Meier et al., 2013; Amson et al., 2022), or rodent taxa (Biknevicius, 1993; Casinos et al., 1993; Pinto et al., 2010; Montoya-Sanhueza and Chinsamy, 2017, 2018; Mielke et al., 2018; Scheidt et al., 2019; Montoya-Sanhueza et al., 2019, 2021), the aardvark *Orycteropus afer* (Legendre and Botha-Brink, 2018), and the wombat *Vombatus ursinus* (Walker et al., 2020).

3.4.1. Mid-diaphyseal limb bone microanatomy

In comparison to strictly terrestrial, cursorial, and arboreal relatives, fossorial taxa generally show stouter stylopods, resulting in relatively shorter, but broader, shafts for digging in hard substrate (Fabre et al., 2015; Amson and Bibi, 2021; Gônet et al., 2023b). Regardless of the digging style, degree of digging activity, body size, and metabolism of the investigated species, most studies mentioned above reported some extent of mid-diaphyseal cortical thickening (and higher global compactness values, in general) in the long bones of adults of fossorial taxa (Fig. 2), as compared to their non-fossorial, surface-dwelling relatives (even in the naked mole rat *Heterocephalus glaber*, which is primarily a chisel-tooth digger; Montoya-Sanhueza et al., 2021). Montoya-Sanhueza and colleagues (e.g., Montoya-Sanhueza and Chinsamy, 2017; Montoya-Sanhueza et al., 2021) further showed that the long bone cortical thickening of fossorial mammals during ontogeny may result from very different modeling processes and subjacent morphogenetic pathways, hence resulting in different bone histologies, despite convergent microanatomical adaptations. For instance, cortical thickening in the Cape dune mole rat (*Bathyergus suillus*) results from an imbalanced modeling during ontogeny, with increased periosteal and endosteal deposition and very limited expansion of the medullary cavity and perimedullary resorption (Montoya-Sanhueza and Chinsamy, 2017; Fig. 2D-G). By contrast, the naked mole rat exhibits considerable expansion of the medullary cavity early in ontogeny, followed by extensive endosteal bone deposition during later development of limb bones (Montoya-Sanhueza et al., 2021). Interestingly, several studies have found that hindlimb bones (in particular the femur) also exhibit high compactness in most fossorial mammals. This may be related to the fact that most scratch-digging species use their hindlimbs not only to remove loose soil, but also to brace the body during digging (Legendre and Botha-Brink, 2018; Parsi-Pour and Kilbourne, 2020; Montoya-Sanhueza et al., 2021; Fig. 2G, J, M).

Other aspects of limb bone cross-sectional geometry have also been the subject of recent studies. Amson and Bibi (2021), for instance, noted that the shafts of fossorial mammals tend to be more elliptical than in non-digging relatives. Hence bats and flying squirrels show rather circular humeral cross sections with relatively thin cortices that favor torsional resistance (see Swartz et al., 1992; Margerie et al., 2005; Amson and Bibi, 2021), but digging mammals tend to show more elliptical and compact humeral cross sections (Fig. 2) that better withstand both bending and axial loading (Margerie et al., 2005; Amson and Bibi, 2021) associated with breaking hard substrate during digging activity. Interestingly, a study by Meier et al. (2013) on talpids did not show a significant difference in cortical bone thickness between moles and non-fossorial relatives of similar sizes. However, the authors reported that the medullary cavity was more elliptical in fossorial talpids than in non-fossorial ones. Similarly, comparative studies suggest that the transition zone between the compact cortex and the free medullary cavity tends to be wider in fossorial mammals as compared to surface-dwelling relatives (Meier et al., 2013, Gônet et al., 2023b; Fig. 2). Such microanatomy can be the outcome of two features that are not mutually exclusive: the presence of bone trabeculae in the medullary region and an uneven cortical thickness within the cross section. Hence, fossorial talpids have greater extension of the medullo-cortical transition in the humerus as compared to terrestrial groups of similar body-sizes (Meier et al., 2013; Gônet et al., 2023b).

3.4.2. Limb bone epiphyseal microanatomy

Two independent studies have observed a greater degree of anisotropy of bone trabeculae (i.e. trabeculae tend to have a preferential orientation) in the humeral epiphyses of fossorial species as compared to their non-fossorial relatives. These studies were conducted on large taxonomic samples in xenarthrans (Amson et al., 2017) and mustelids (Amson and Kilbourne, 2019). Additionally, Amson et al. (2022) found that, despite notable disparity between fossorial mammals, subterranean species differ from the other sampled species in featuring significantly higher bone fraction in their humeral head. These observations suggest that not only the midshaft, but also the epiphyseal structure of long bones can yield a functional signal related to digging.

3.4.3. Limb bone mid-diaphyseal histology

The cortical bone histology of extant fossorial mammals is highly variable, depending on the species, the ontogenetic stage, and the skeletal element considered. Montoya-Sanhueza and Chinsamy (2017) reported on unusually large amounts of compacted coarse cancellous

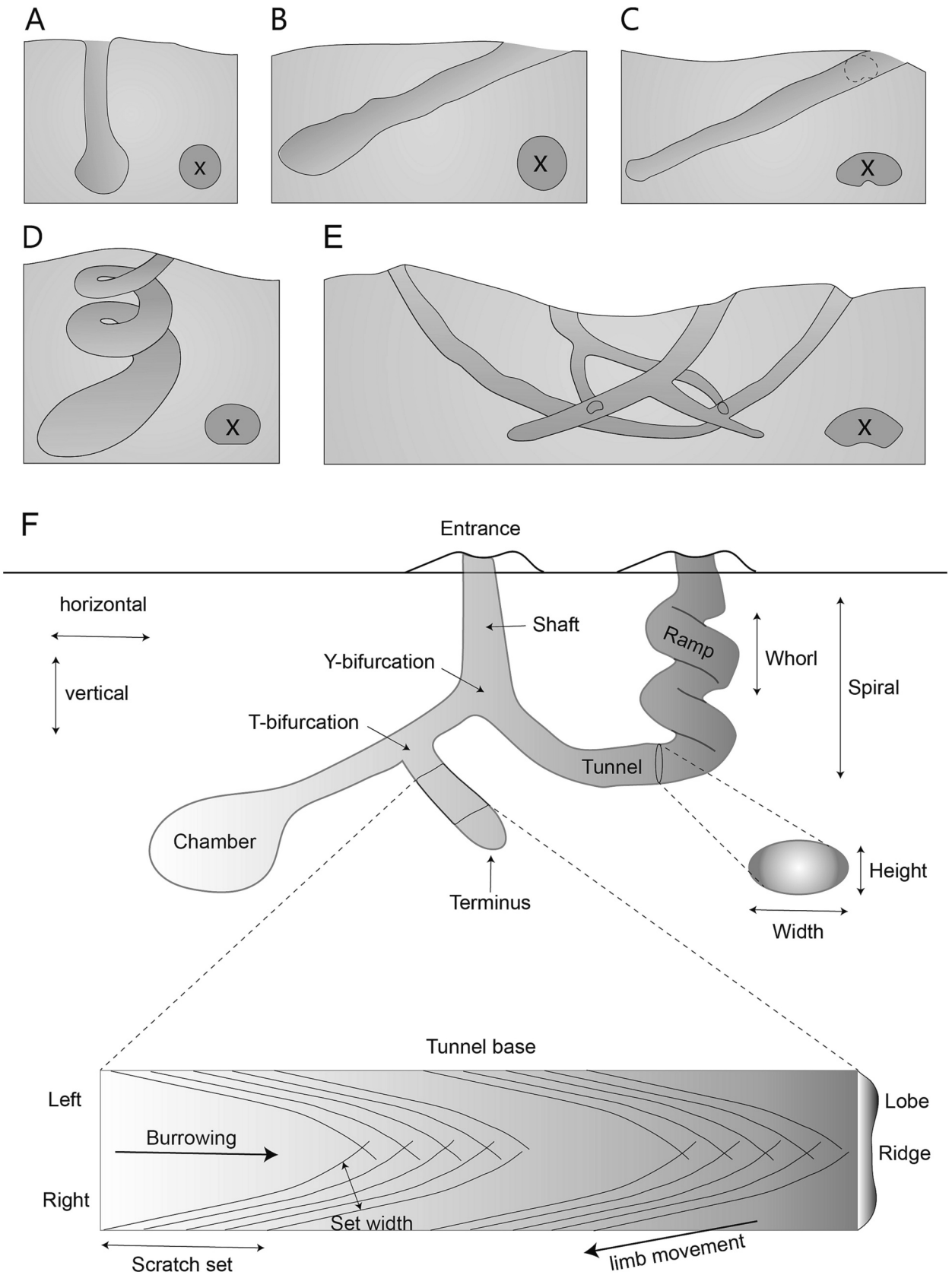

Fig. 3. Vertebrate burrow structure and terminology. A) Sub-vertical burrows, circular section. B) Low-angle burrows ending in enlarged chamber, circular section. C) Low-angle burrows with kidney-shaped section. D) Spiral burrows ending in enlarged chamber, plano-convex section. E) Complex burrow system with tunnel branching, tapering tunnel terminations and kidney-shaped section. F) Burrow terminology.

bone (CCCB) in the humeral and femoral shafts of adult cape mole rats (*Bathyergus suillus*; Fig. 2H). Such tissue, formed in the early stages of ontogeny, is usually only found in the metaphyses of limb bones, not in the mid-diaphysis, as it gets resorbed with the expansion of the medullary cavity (Enlow, 1963). Montoya-Sanhueza and Chinsamy (2017) concluded that the presence of compacted coarse cancellous bone in the midshafts of *B. suillus* stylopods is related to specific modeling processes (e.g. cortical drift) and does not constitute a unique adaptation to fossoriality. Important quantities of compacted coarse cancellous bone were subsequently documented in several fossorial mammalian species, such as the aardvark (*Orycteropus afer*; Legendre and Botha-Brink, 2018; Fig. 2K), various armadillos (Straehl et al., 2013; Heck et al., 2019; Fig. 2N), the wombat (*Vombatus ursinus*; Walker et al., 2020), and highly fossorial talpids (Amson et al., 2022). These recurrent observations led some researchers to question its adaptive significance in relation to digging behaviours (Legendre and Botha-Brink, 2018; Amson et al., 2022). Due to its microstructure, this bone is classically seen as very compliant and could provide extra resistance to strong bending constraints during digging, as hypothesized by Legendre and Botha-Brink (2018). However, large amounts of compacted coarse cancellous bone have also been reported in semi-aquatic (Geiger et al., 2013; Canoville and de Buffrénil, 2016; Buffrénil et al., 2021) and even volant taxa (Ricqlès et al., 2000; Prondvai et al., 2012). Hence, the presence of CCCB alone cannot be considered as an indication of fossoriality.

3.4.4. Vertebral microanatomy

In a preliminary analysis testing for the relationship between vertebral microanatomy and lifestyle in squamates, Houssaye et al. (2010) found that vertebrae of fossorial taxa are generally denser than those of terrestrial relatives. In mammals, Amson and Bibi (2021) found that vertebral structural parameters are mostly influenced by body size. They nonetheless noted that many subterranean species are characterised by a greater number of trabeculae than expected for their size, as well as a higher degree of anisotropy (orientation of trabeculae) as compared to non-fossorial taxa.

4. Early vertebrate fossoriality

4.1. Morphology and ichnotaxonomy of fossil vertebrate burrows

The morphological diversity of fossil burrows is similar to that observed in burrows of modern-day taxa, therefore a similar use can be hypothesized. Two main types of structures can be distinguished in fossil vertebrate burrows: i) sub-vertical or high-angle, simple burrows (Fig. 3A) and ii) sub-horizontal or low-angle, simple to complex burrows (Fig. 3B-E). The high-angle simple burrows do not branch, have circular or elliptical cross-sections, are straight to slightly curved, and some can taper distally or have a terminal enlarged part (Fig. 3A). They are generally considered aestivation structures by comparison with modern structures (e.g., Greenwood, 1986). The low-angle burrows can have circular or elliptical cross-sections. The roof is generally convex, the floor can be convex, flat, or with a central ridge (Fig. 3B-E). In cases where a medial ridge is present, the cross-section can be reniform (Krummeck and Bordy, 2018). The tunnels constituting the burrow can be straight (Fig. 3B-C), curved, sinusoidal, or spiral (Fig. 3D). Although the overall spiral structure can develop vertically, the tunnel angle is still low, therefore these structures are considered low-angle. In some cases, branching is observed, which generates more complex structures (Fig. 3E). Tunnels can taper distally (Fig. 3E), have a rounded but not tapering termination (Fig. 3C), or have an enlarged termination (Fig. 3B, D).

Scientists studying vertebrate burrows have a specific terminology and use a specific set of measurements to describe burrow architecture that are worth reviewing here briefly (e.g., Hasiotis et al., 2007; Bordy et al., 2019). Horizontal and vertical refer to the orientation of the surface in which the burrow was excavated (Fig. 3F). Top, bottom, and side can be used to refer to the burrow or burrow parts. The openings at the top surface are called entrances (Fig. 3F). The vertical parts are called shafts, the horizontal parts tunnels (Fig. 3F). The asymmetrical shafts have maximum and minimum diameter, the tunnels have height and width (Fig. 3F). There can be low-angle spiral (or helical) tunnels; a complete round of a spiral is called a whorl and the descending tunnel is called a ramp (Fig. 3F). There can be tunnel branchings, called bifurcations. Bifurcations can be of different types depending on the branching angle; Y is less than 90°, T and X are about 90° (Fig. 3F). The simple tunnel termination is called a terminus, whereas the enlarged tunnel termination is called a chamber (Fig. 3F), which can be simple or have lobes. Sub-horizontal burrows commonly show digit scratch traces, usually organized in bilateral sets up to 4 or 5 parallel impressions, which can be straight, curved, short, or relatively long (Fig. 3F). A high degree of overlap of these traces makes the interpretation of the sets sometimes difficult, sometimes generating rhomboid patterns (Krummeck and Bordy, 2018). The scratch traces are commonly preserved on the base (Fig. 3F) or the sides of the structures, but can also be found on the roof. Left and right refer to the burrowing direction, and ridges and lobes are structures that can be found on the bottom of the tunnel (Fig. 3F).

Typical burrow measurements include minimum and maximum diameter for sub-vertical burrows and shafts, minimum and maximum height and width for sub-horizontal burrows and chambers, and height and areal extension of the whole structure for complex burrows (e.g., Hasiotis et al., 2007). Additional measurements, such as the sinuosity index, can be taken for spiral and sinusoidal burrows (e.g., Smith, 1987; Voigt et al., 2011), and other parameters such as volume can be calculated. As regards scratch sets (or clusters), their width can be measured in points where the scratch traces are parallel, and also single scratch traces can be measured in length and width, as well as the width between adjacent scratches in the same set (Bordy et al., 2019).

Fossil vertebrate burrows are classified in parataxonomic ichnogenera and ichnospecies according to the rules of the ICZN (1999), independent from the systematics of their potential producers. For the Carboniferous–Triassic, ichnotaxa have been established for relatively simple structures such as sub-vertical simple burrows (e.g., *Cornulatichnus edayensis* Carroll and Trewin, 1995, *Torridorefugium eskridgensis* Hembree et al., 2005, *Redondarefugium abercrombieorum* Lucas et al., 2010) or sub-horizontal simple burrows with a ridge on the floor (*Reniformichnus katikatii* Krummeck and Bordy, 2018, *Reniformichnus australis* McLoughlin et al., 2020) (Table 1). However, the ichnotaxonomy of more complex structures is still lacking (e.g., Groenewald et al., 2001; Voigt et al., 2011; Fiorelli et al., 2018).

4.2. Taphonomy of fossil vertebrate burrows

Fossil vertebrate burrows can be preserved in different depositional settings. In alluvial environments, burrows are generally preserved in abandoned channel deposits (e.g., Bordy et al., 2011; Voigt et al., 2011; Krapovickas et al., 2013), crevasse splay deposits (e.g., Bordy et al., 2019), and floodplain deposits (e.g., Smith, 1987; Groenewald et al., 2001; Miller et al., 2001; Sidor et al., 2008; Storm et al., 2010; Bordy et al., 2011; Colombi et al., 2012; Krummeck and Bordy, 2018). They can also be preserved in ephemeral lake deposits (e.g., Hembree et al., 2004; McLoughlin et al., 2020) and aeolian dune deposits (Francischini et al., 2023). Often, they are associated with signs of: i) pedogenic alteration implying weathering and ii) subaerial exposure, such as mud cracks and/or raindrops on the surface with the burrow entrance (e.g., Hembree et al., 2005; Fiorelli et al., 2018).

Vertebrate burrows are originally hollow structures excavated by fossorial animals in unconsolidated sediments such as sand, silt, mud, or soil with one or multiple entrances. Burrows remain either hollow during their use or collapse immediately after the passage of the animal (Hildebrand, 1985). During burial, the empty structures either collapse or are filled-in passively by new sediment brought in by flooding or

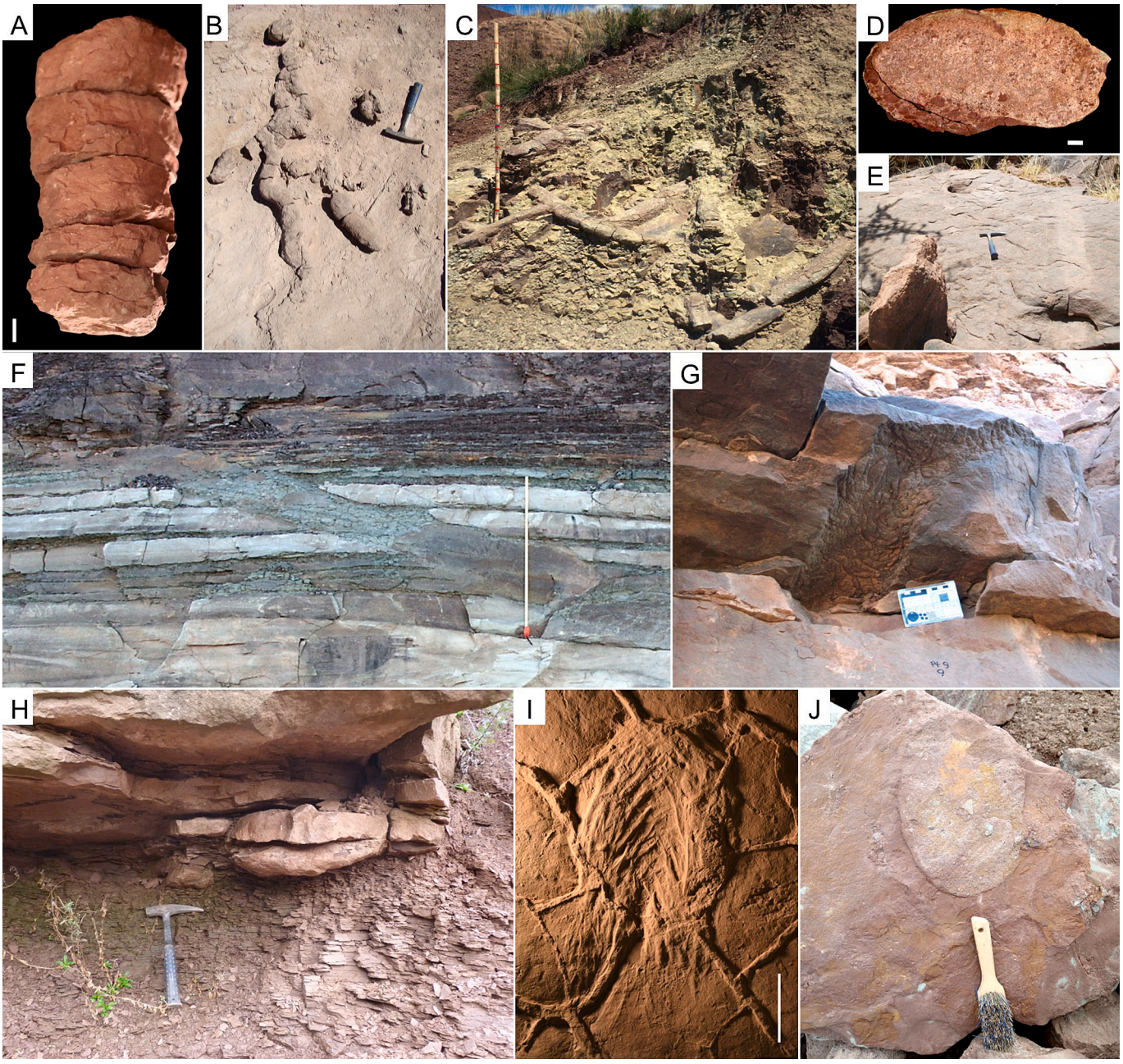

Fig. 4. Preservation of vertebrate fossil burrows. A) FMNH-UF 1039. Sub-vertical burrow infill preserved in disk-shaped parts. Vale Formation, Cisuralian, Texas. Scale bar = 1 cm. B) Burrow infill preserved in a pedogenized sandstone. Chañares Formation, Late Triassic, Argentina. Photo courtesy of L.E. Fiorelli. C) Burrow infill preserved in mudstone. Burgersdorp Formation, Early Triassic, South Africa. Photo courtesy of G.H. Groenewald. D) BP/6/698. *Reniformichnus katikatii*, holotype. Burrow infill section showing normal grading of the sediment. Scale bar = 1 cm. Katberg Formation, Early Triassic, South Africa. Photo courtesy of E.M. Bordy. E) Two burrow entrances on the top of a sandstone layer. Timezgadiouine Formation, Middle Triassic, Morocco. Photo courtesy of H. Saber. F) Burrow cutting sandstone layers, vertical section, lateral view. Katberg Formation, Early Triassic, South Africa. Photo courtesy of E.M. Bordy. G) Burrow in sandstone layer, burrow roof. Timezgadiouine Formation, Middle Triassic, Morocco. Photo courtesy of H. Saber. H—I) Tambach Formation, Cisuralian, Germany. H) MNG-16804. Burrow chamber between sandstone and mudstone layers, front view. I) MNG-16387. Two rows of scratch trace sets at the bottom of a burrow infill, convex hyporelief, plaster cast. Scale bar = 10 cm. J) MfNMD P-22249. Burrow section on the bottom of a sandstone layer. Lopingian, Germany.

wind. Over time, this generates a burrow infill or burrow cast that can lithify, and also can be modified by diagenetic processes. In cases of burrow collapse and infill with sediment identical to the host rock, burrows may not be recognisable or only in a limited way; this can enhance difficulties in the interpretation of the burrow structure and in the estimation of the original burrow density (e.g., Smith, 1987; Bordy et al., 2019).

In sub-vertical burrows, the burrow infill commonly preserves as superimposed disc- or checker-like structures (e.g., Olson and Bolles, 1975) (Fig. 4A). Burrows can be preserved in soils, such as the burrow infill in weathered sandstone of Fig. 4B (Fiorelli et al., 2018). The burrow infill can have a different composition and grain size compared to the host rock, such as the complex burrow system cast of fine-grained sandstone in a mudstone host rock of Fig. 4C (Groenewald et al., 2001). The passive infill generally shows normal grading, so coarser sediment at the base (sometimes with rip-up clasts) and progressively finer towards the top because of the progressively lower flood energy (e.g., Krummeck and Bordy, 2018) (Fig. 4D). The burrow can be completely or

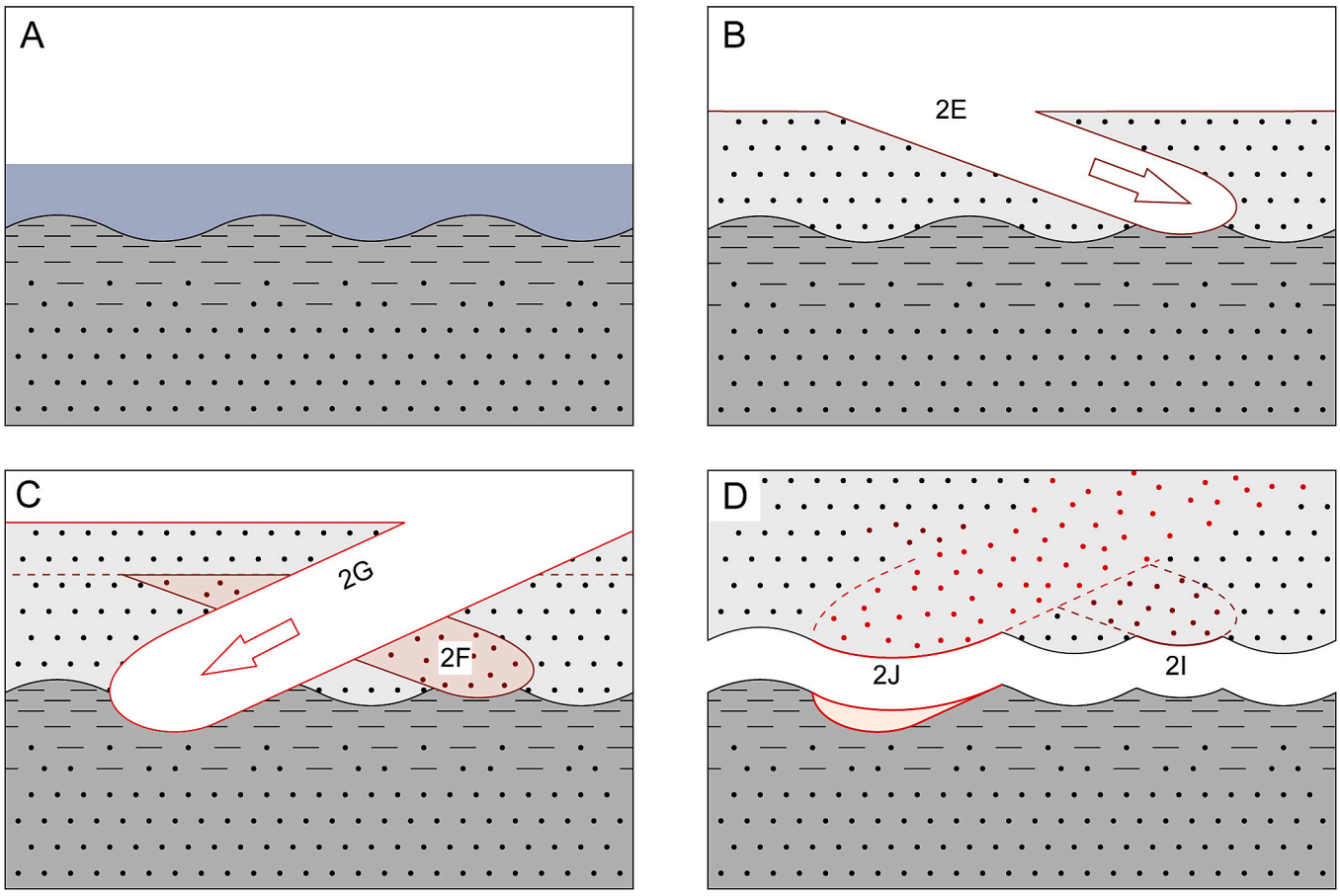

Fig. 5. Preservation of vertebrate fossil burrows. A) Sediment deposition. B) Low-angle vertebrate burrow excavated in a sandstone and reaching the underlying mudstone (Fig. 2E). C) Low-angle vertebrate burrow excavated in the sandstone (Fig. 2G), cutting the infill of the other low-angle burrow (Fig. 2F) and reaching the mudstone. D) The bottom of the sandstone layer is exposed, showing the bottom of the first burrow (Fig. 2I) and a section of the second burrow (Fig. 2J). Arrows represent the burrowing direction.

partially filled in, and this can happen through one or multiple flooding events (each showing grading). After diagenesis, it is possible to find the original cavity and/or the natural cast, which can be preserved three-dimensionally (Groenewald et al., 2001) (Fig. 4C). The most common case is finding different burrow parts separately and/or only partly visible, which makes the interpretation challenging. It is possible to find burrow entrances on a surface (Voigt et al., 2011) (Fig. 4E), low-angle tunnels cut vertically along the burrow direction (Bordy et al., 2011) (Fig. 4F), burrow roofs visible from the bottom side (Voigt et al., 2011) (Fig. 4G), burrows at the interface of different lithologies, such as a mudstone/sandstone transition (Fig. 4H), burrow bottoms with scratch traces preserved in convex hyporelief (Fig. 4I), and burrow sections cut perpendicularly to the burrow direction (Fig. 4J). The scheme in Fig. 5 shows, as an example, the mechanism of preservation of hypothetical low-angle vertebrate burrows excavated within sand with underlying mud. After a first flood (Fig. 5A), sand is deposited over the mud layers. Subsequently, the surface is exposed to the air and the sand is burrowed. This burrow reaches the bottom of the sand and touches the underlying mud layer (Fig. 5B). A second flood follows, deposits sand over the surface and fills in the burrow. A second low-angle burrow is excavated through the new and old sand layers, cuts the older burrow infill, and reaches the mud (Fig. 5C). After diagenesis and exhumation, the upper surface of the mudstone and the lower surface of the sandstone are exposed (Fig. 5D). Only the bottom of the older burrow and a section of the younger burrow are visible.

4.3. *Identifying the producer of fossil vertebrate burrows*

4.3.1. *Discriminating vertebrate from invertebrate burrows*

The confident attribution of continental burrows to either vertebrate or invertebrate producers can be challenging, because the producer is usually not preserved and structures made by both groups have a significant overlap in terms of morphology and size. Nevertheless, size is often used as a determining criterion in the ichnological literature, as tetrapod burrows are generally wider than 1 cm and usually more than 5 cm, while invertebrate burrows are commonly less than 1 cm wide (e.g., Buatois et al., 2017). However, relatively large invertebrate burrows of arthropod origin are also known (e.g., *Taenidium barretti*, up to 25 cm wide; Keighley and Pickerill, 1994). A more reliable feature is the presence of reworked sediment, i.e., active backfill testified by the occurrence of meniscate structures (Fig. 6A), which are typical of invertebrates such as arthropods packing the sediment backwards while burrowing (although exceptions exist, see Melchor et al., 2012). Vertebrate burrows are instead usually passively infilled, as indicated by sediment grading (Fig. 4D).

Another typical feature of invertebrate burrows is the presence of wall linings, striae (Fig. 6B-C), and pellets, which are absent in vertebrate burrows (e.g., Keighley and Pickerill, 1994). Striae are invertebrate scratch traces (produced by six or more limbs): generally thin, long, and covering the entire external surface of the burrow cast. Scratch traces of limbed vertebrates are different, because they are generally arranged in two parallel rows of straight to curved scratch sets, each set up to five traces (produced by the digits of the autopodia).

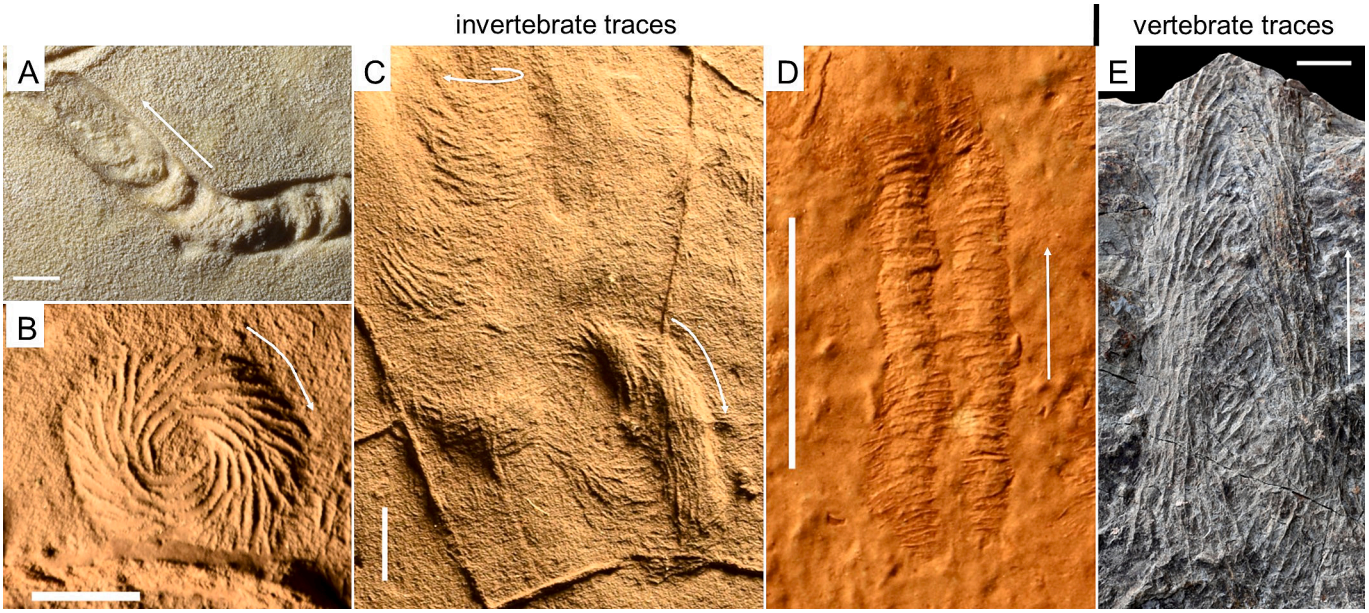

Fig. 6. Differences between vertebrate and invertebrate trace fossils. A) MNA-N 3686. *Taenidium* with meniscate back-filling structures, resin cast. Coconino Sandstone, Cisuralian, Arizona. B—C) *Tambia spiralis*. Tambach Formation, Cisuralian, Germany. B) MNG-8996. Bottom view of a spiral tunnel showing parallel lineation, convex hyporelief. C) MNG-10106. Lateral view of a spiral tunnel and bottom view of spiral whorls showing parallel lineation, convex hyporelief. D) HU-F 205. *Cruziana problematica*. Two rows constituted by horizontal narrowly-spaced traces, convex hyporelief. Choza Formation, Cisuralian, Texas. E) Vertebrate scratch trace sets. Two rows constituted by sets of up to 5 scratch traces each parallel to the burrowing direction and distally converging towards the midline. Convex hyporelief on the bottom of a sandstone layer. Burgersdorp Formation, Middle Triassic, South Africa. Scale bars A-D = 1 cm, E = 10 cm. Arrows represent the supposed trace fossil direction.

Other than sub-vertical aestivation burrows, vertebrates usually produce sub-horizontal structures with short vertical shafts. Spiral shafts are the exception, but also in this case the spiral is usually low-angle. Conversely, invertebrates commonly excavate long, vertical shafts above sub-horizontal tunnels (e.g., crayfish burrows, Hasiotis et al., 1993, 1999). Moreover, sub-horizontal or spiral vertebrate burrows usually have an elliptical section, whereas invertebrate burrows more commonly have a circular section (e.g., Hasiotis et al., 1999). Also, the occurrence of a medial ridge on the bottom of the tunnel can be an indication of a tetrapod producer (e.g., Damiani et al., 2003; Krummeck and Bordy, 2018). A final, optimal indication of the producer is the finding of its remains within the burrows, in life position, which is however rare (e.g., Damiani et al., 2003).

In short, the main features that allow a distinction between vertebrate and invertebrate burrows are: size, presence/absence of meniscate structures, lineations, striae, scratch trace sets, tunnel inclination, vertical shaft length, cross section shape, and fossil content.

A remarkable example of vertebrate/invertebrate producer uncertainty is *Taenidium barretti*, an abundant ichnotaxon in Silurian, Devonian, and Carboniferous continental units of Europe, North America, and Antarctica (e.g., Allen and Williams, 1981; Graham and Pollard, 1982; Gordon, 1988; Bruck et al., 1985; Morrissey and Braddy, 2004). This ichnospecies was originally classified as *Beaconites barretti* Bradshaw, 1981, prior to revision by Keighley and Pickerill (1994), who transferred it to the ichnogenus *Taenidium*. Various authors have proposed a vertebrate (e.g., Archer in Scott et al., 1976; Donovan et al., 1978) or even a tetrapod producer for *Taenidium* specimens (Ridgeway, 1974; Pollard, 1976), based in part on their large size, while others suggested worms or arthropods (Laming, 1970; Gevers et al., 1971; Müller, 1975; Rolfe, 1980; Allen and Williams, 1981). Although the overall burrow shape, being unbranching, tubular, and vertical-to-gently-curved relative to the substrate, resembles lungfish burrows (e.g., Benton, 1988), the occurrence of well-defined arcuate menisci is not in agreement with a lungfish producer, but rather with an arthropod producer (e.g., Morrissey and Braddy, 2004; Pearson and Gooday, 2019) (Fig. 6A). In addition, the morphology of burrow turns and the association with arthropod trackways of similar width (*Diplichnites*, attributed to arthropleurid 'giant millipedes') from the same units support this interpretation.

Similarly, the small-sized ichnotaxon *Tambia spiralis* has been attributed to arthropod (Knaust et al., 2022), annelid (Müller, 1969), or small tetrapod (Martens, 2001a, 2001b, 2005) producers. Knaust et al. (2022) interpreted this structure as an arthropod burrow rather than an annelid, because of the striae. The interpretation of *Tambia spiralis* as a tetrapod trace was not justified and is inconsistent with the size of the tunnels (around 1 cm wide) and with the morphology and arrangement of striae. They are in fact parallel and distributed uniformly on the external surface of the burrow (Fig. 6B-C). This is inconsistent with scratch traces produced by a tetrapod, which would instead produce rows of bilateral sets of up to five scratch traces each (e.g., Bordy et al., 2019).

The fossil traces from the Middle Triassic part of the Burgersdorp Formation of South Africa, initially assigned to very large examples of the invertebrate trace *Cruziana* by Shone (1978), constitute another example of problematic identification. Typical *Cruziana* striations are perpendicular to the trace direction, do not form sets, and tend to become less perpendicular towards the middle of the trace (Fig. 6D); this is not observed in the material described by Shone (1978). Bordy et al. (2019) revised this material and noticed clear differences from *Cruziana*, such as the two parallel rows of scratch sets that converge towards the middle of the trace (angle of 10–50°), forming lobes. The parallel rows of scratch sets (up to five scratches each) that converge, can form lobes, and obliterate previous scratch sets observed in the Burgersdorp traces (Fig. 6E) are typical of animals with bilateral symmetry and five digits in the autopodia, i.e., tetrapods such as therapsid synapsids (e.g., Buchwitz et al., 2018).

4.3.2. *Identifying the vertebrate producer taxon*

Identifying the exact producers of fossil vertebrate burrows can be challenging, because usually no skeletons are found within, and even

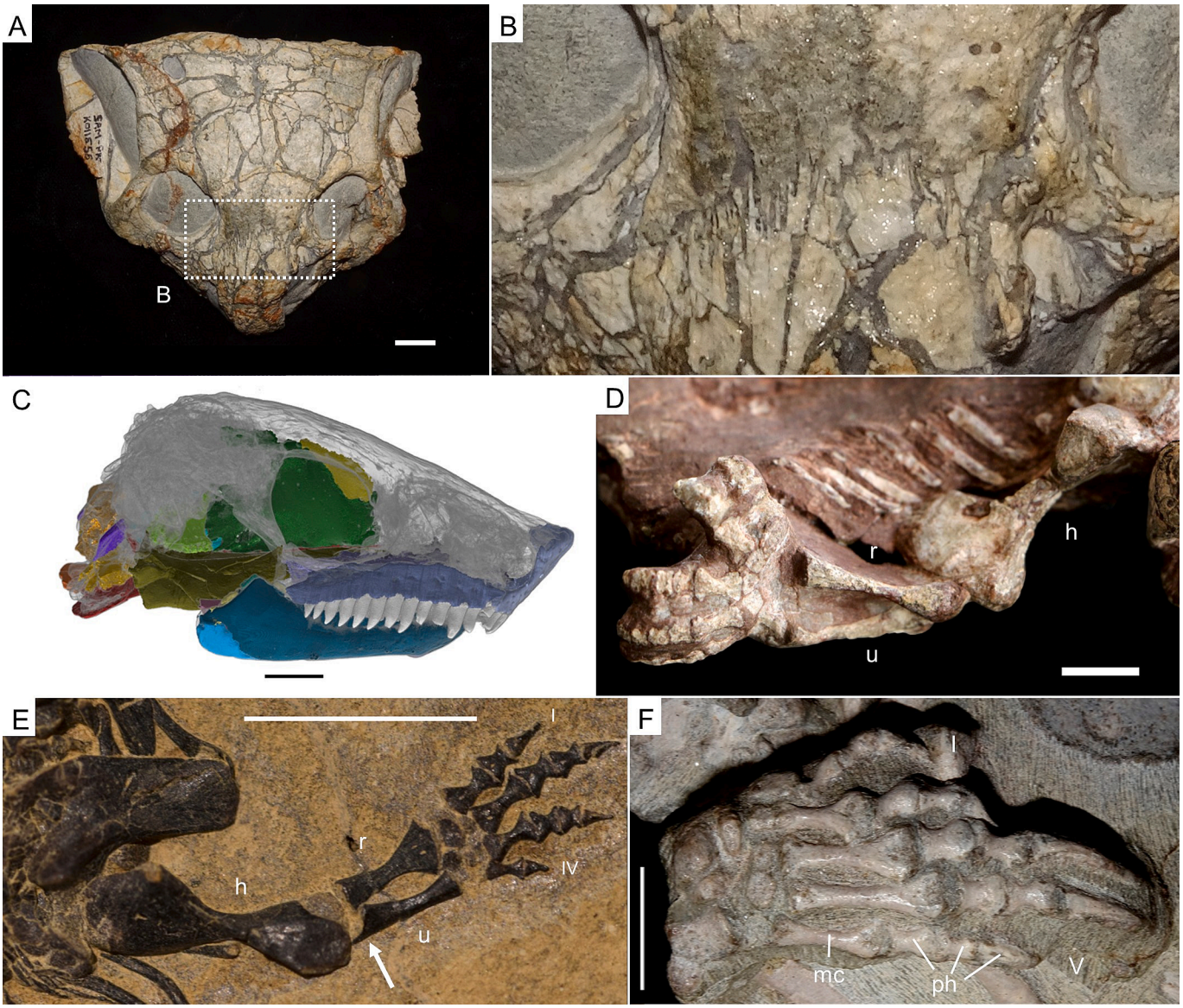

Fig. 7. Skeletal morphological features associated to fossoriality in extinct taxa. A) SAM-PK-K11555. *Cistecephalus microrhinus*. Skull, dorsal view. Note the triangular shape. Scale bar = 1 cm. Lopingian, South Africa. B) Enlargement of A. Highly interdigitated cranial sutures. C) OMNH 73107. *Nannaroter mckinziei*. Skull, lateral view showing the prominent rostrum, 3D model from CT scan. Scale bar = 2 mm. Richard Spur, Cisuralian, Oklahoma. D) NHMUK PV R4087. *Procolophon trigoniceps*. Left spatula-shaped forelimb, dorsal-lateral view. Scale bar = 1 cm. Early Triassic, South Africa. E) MNHM PW 2001/307-LS. *Batropetes palatinus*. Right forelimb, dorsal view. The arrow indicates the prominent olecranon process. Scale bar = 5 mm. Meisenheim Formation, Cisuralian, Germany. F) AM 3677. *Tetracynodon darti*. Right forelimb with large terminal phalanges, dorsal view. Katberg Formation, Early Triassic, South Africa. Scale bar = 1 cm. h = humerus, r = radius, u = ulna, mc = metacarpal, ph = phalanx. I, IV, V = digit number.

when this is the case, it does not necessarily mean that the individual generated the structure (e.g., Fernandez et al., 2013). In fact, animals can use pre-existing structures, to the point that an entire ecosystem can be heavily dependent on burrows excavated originally by a single taxon, i.e., the ecosystem engineer (e.g., Mukherjee et al., 2017; Doody et al., 2021). Moreover, animal carcasses can be washed into the burrow by a flood or can be brought into the burrow by predators or scavengers (e.g., Modesto and Botha-Brink, 2010). Therefore, it is important to evaluate the taphonomy of the find and also the occurrence of fossorial features in the skeleton of the potential producers found within the burrow or in the associated local fauna. More commonly, no skeletons are found within the burrows. In this case, most studies rely on burrow size and morphology compared to skeletons found in the same unit (e.g., Fiorelli et al., 2018) or in stratigraphically equivalent units (e.g., Sidor et al., 2008; Francischini et al., 2023). Some studies even consider the inferred producers of trackways found in the same stratigraphic unit (Voigt et al., 2011). In all studies, particular attention is given to taxa that are supposed to be fossorial based on macro- and micromorphological features.

4.4. Taphonomy of vertebrate remains within fossil burrows

Finding skeletal remains within burrow infills is relatively uncommon, but multiple cases are described in the literature. Generally, skeletons can be either articulated or disarticulated. In fossil sub-vertical simple burrows, they can be found in what is inferred to be their life position. This includes a sub-vertical orientation with the tail pointing towards the burrow end (*Gnathorhiza* lungfish burrows; Dalquest et al., 1989) or body arranged in a coiled position (*Brachydectes* "microsaur" burrows; Hembree et al., 2004). In sub-horizontal burrows, examples of disarticulated skeletons found in the burrow infill include the dicynodonts *Diictodon* and *Lystrosaurus* from South Africa (Modesto and Botha-Brink, 2010; Smith et al., 2021). Complete skeletons are generally

found in a dorsal-up position, with the head directed towards the burrow termination. This case is observed for the cynodont *Thrinaxodon* (e.g., Damiani et al., 2003) and the dicynodont *Lystrosaurus* (Botha-Brink, 2017). Other occurrences show curled-up skeletons at the burrow termination, such as for the dicynodont *Diictodon* (Smith, 1987) and the theriodonts *Langbergia* (Groenewald et al., 2001; Abdala et al., 2006a, 2006b) and *Microgomphodon* (Wolvaardt, 2021). In some other cases, the skeleton can be found in ventral-up position, suggesting transport, such as the temnospondyl *Broomistega* found in a ventral-up position above a *Thrinaxodon* skeleton, preserved instead in a dorsal-up position (Fernandez et al., 2013). Skeletons preserved in peculiar poses and associations have also been interpreted as potentially being in a burrow, although the original structure is not preserved (e.g., Abdala et al., 2006a, 2006b). This includes curled-up skeletons (e.g., Olson and Bolles, 1975; Smith, 1987) and associations of tightly-packed skeletons (e.g., Smith et al., 2021).

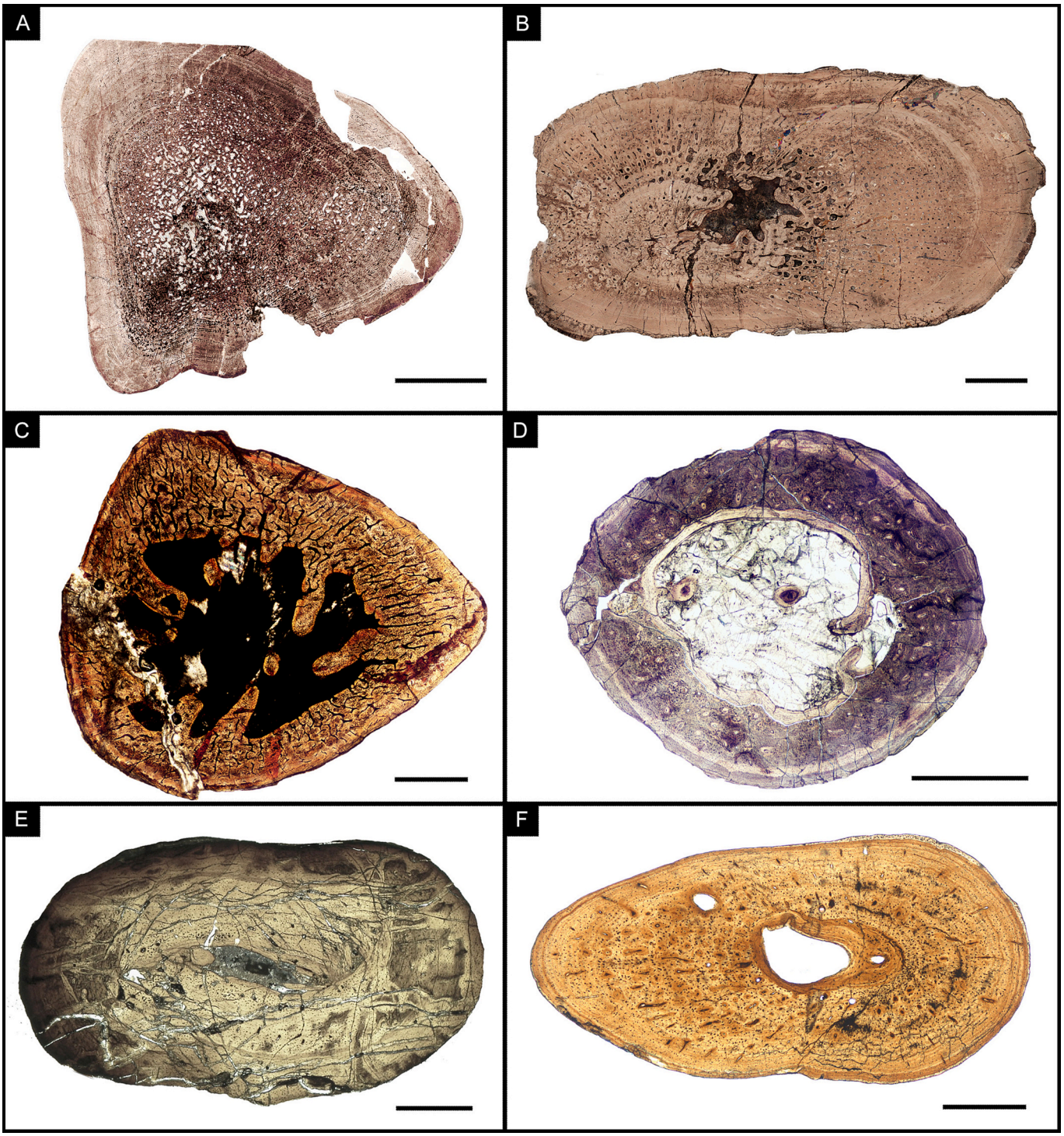

Fig. 8. Mid-diaphyseal limb bone cross-sections of selected extinct taxa hypothesized to have been at least partly fossorial. A) *Lystrosaurus maccaigi* NMQR 3663a humerus. B) *Oudenodon bainii* SAM-PK-K4807A femur. C) *Thrinaxodon liorhinus* BP/1/5208 humerus. D) *Thrinaxodon liorhinus* BP/1/5208 radius. E) *Pappochelys rosinae* SMNS 91357 Femur. F) *Eunotosaurus africanus* USNM 23099 ulna. Scale bars equal 10 mm in A; 2 mm in B; 1 mm in C, D; 0.5 mm in E, F. Images A to D were provided by J. Botha; E by R. Schoch, T. Scheyer and N. Klein; F by T. Lyson.

4.5. Morphological features associated with fossoriality in fossil vertebrates

Morphological adaptations associated with fossoriality in vertebrates are generally separated into two categories, cranial and postcranial. As in extant analogues, hypothesized fossoriality in extinct taxa may exhibit features from both or only one of these categories depending on the types of digging behaviour employed.

4.5.1. Cranial adaptations

Vertebrates that utilize their skull for digging (e.g., head-lift digging, chisel-tooth digging), and even those that rely primarily on their limbs, often have adaptations that help to better reinforce or support the skull. The modification of neurocranial elements into larger compound units, to better withstand compressive forces, is a characteristic change to the skull observed in fossil caecilians (Maddin et al., 2012) and recumbirostran "microsaurs" (Pardo et al., 2015). Highly interdigitated cranial sutures are another adaptive feature documented in fossil taxa that are considered fossorial, such as the dicynodont synapsid *Cistecephalus* (Keyser, 1973; Kammerer, 2021) (Fig. 7A-B). Head-lift digging is a common fossorial mode that can be associated with short triangular skulls, as is also observed in *Cistecephalus* (Fig. 7A). Head-lifting has been ascribed to various extinct tetrapods, such as the recumbirostran "microsaurs" (e.g., Pardo et al., 2015). These commonly show a broad spatulate head and a mouth shifted inferiorly, as in the taxon *Nannaroter* (Fig. 7C). Teeth may also be used in digging, with chisel-tooth digging having been ascribed to Oligocene and Miocene burrowing beavers because of their long, deeply implanted incisors (Samuels and Valkenburgh, 2009).

4.5.2. Postcranial adaptations

The forelimbs can be modified in a variety of ways to accommodate a fossorial lifestyle, and this is evident in the skeleton of fossorial animals. In many cases, shovel-like forelimbs, very broad, shortened phalanges, and very broad unguals can be observed (Hildebrand, 1974, 1985). These manual morphologies are also observed in, for instance, extinct procolophonid reptiles (e.g., MacDougall et al., 2013) (Fig. 7D). Other features include robust humeri with large medial epicondyles and ulnae with large olecranon processes, such as those observed in the recumbirostran *Batropetes* (Glienke, 2012, 2015) (Fig. 7E) and cistecephalid dicynodonts (Cluver, 1978). Numerous digging animals make use of their claws for digging, and as a result many have modifications to their unguals and associated phalanges. Generally, proximal phalanges are usually short and thick and unguals can be long and laterally compressed (e.g., MacLeod and Rose, 1993). This is observed in therocephalians such as *Tetracynodon* (Fontanarrosa et al., 2019) (Fig. 7F) and cistecephalid dicynodonts (Cluver, 1978). Reduction of the length of non-ungual phalanges is also observed in some fossorial tetrapods (Hildebrand, 1985). In extinct taxa, this is known in the recumbirostran *Batropetes* (Glienke, 2012, 2015) (Fig. 7E). Some fossorial animals reduce digits or lose their entire limbs to accommodate a fossorial lifestyle (Hildebrand, 1974; Gans, 1973, 1975), as is observed in recumbirostrans and temnospondyls (Mann et al., 2022; Kligman et al., 2023). Aside from the limbs, other parts of the postcranial skeleton can be modified for fossoriality. Broadened dorsal ribs are observed in several fossorial animals. Perhaps the most famous extinct example of this feature is in the early Permian diapsid *Eunotosaurus* (Lyson et al., 2016). Some extant tetrapods use hind feet-first digging, entering the substrate in reverse (Emerson, 1976), but this type of digging behaviour has not currently been ascribed to any early tetrapod.

4.6. Osteohistological indications for fossoriality in fossil vertebrates

Given the occurrence of tetrapod fossil burrows recovered from Permian and Triassic continental deposits, researchers hypothesized that extinction rates across the Permo-Triassic boundary may have been lifestyle-dependent, and that fossorial adaptations as well as specific growth-strategies may have enhanced survival in the unpredictable conditions of the post-extinction Early Triassic (Canoville and Chinsamy, 2015; Botha-Brink et al., 2016; Botha-Brink, 2017). The long bone microstructure of so-called "disaster taxa", as well as Early Triassic species, has thus been the focus of extensive research in order to test, among others, the hypothesis of a widespread fossorial lifestyle in these groups.

For instance, the limb bone microstructure of the Permo-Triassic dicynodont *Lystrosaurus* has been well investigated. A relatively high limb bone compactness, resulting from thick cortices and bone trabeculae in the medullary cavity (see Fig. 8A), has been alternatively related to amphibious, aquatic, or fossorial habits (e.g., Germain and Laurin, 2005; Ray et al., 2005; Canoville and Laurin, 2010; Han et al., 2021). Consideration of the skeletal morphology, occurrence data, and the recovery of *Lystrosaurus* skeletons within burrow structures (Botha-Brink, 2017) allowed Botha (2020) to unambiguously link *Lystrosaurus*' bone microstructure to a fossorial lifestyle (see discussion in Botha, 2020).

High limb bone compactness due to relatively thick bone cortices has been also reported in other late Permian to Middle Triassic therapsids, such as *Diictodon* (Ray and Chinsamy, 2004), *Cistecephalus* (Nasterlack et al., 2012), *Oudenodon* (Botha, 2003; Fig. 8B), *Trirachodon* (Botha and Chinsamy, 2004), and *Thrinaxodon* (Botha and Chinsamy, 2005; Fig. 8C, D), as well as some procolophonids (Botha-Brink and Smith, 2012) and a lydekkerinid temnospondyl (Canoville and Chinsamy, 2015). Such microanatomical adaptations have also been interpreted as functionally related to some degree of burrowing behaviour, in the light of additional morphological or taphonomic observations.

Bone microstructure has also been considered to support the fossorial hypothesis for the origin of turtles. The broadened ribs of the purported stem-turtles *Eunotosaurus africanus* (middle Permian of South Africa) and *Pappochelys rosinae* (Middle Triassic of Germany) are conspicuous features shared by burrowing tetrapods (Jenkins Jr., 1970; Lyson et al., 2013, 2016; Schoch et al., 2019). Lyson et al. (2016) hypothesized that such enlarged ribs conferred thoracic rigidity and functioned initially as trunk reinforcement during digging. Later in the evolutionary history of turtles, these ribs fused together to form the carapace. In agreement with a fossorial lifestyle, *Eunotosaurus* features compact ribs and relatively robust and compact limb bones (Lyson et al., 2016; Fig. 8F). Schoch et al. (2019) also described the microanatomy of *Pappochelys*. The dense femur (Fig. 8E), as well as dense ribs and vertebrae, were considered as evidence for predominantly amphibious or fossorial habits in this taxon (Schoch et al., 2019). The palaeoenvironmental context of *Eunotosaurus* and *Pappochelys* supports a non-marine origin for these dense skeletal elements. The presence of dense skeletal elements might have favored adaptation to an aquatic lifestyle in later-occurring stem and crown-group turtles, however (Lyson et al., 2016).

5. Early vertebrate burrowing record

5.1. Devonian

5.1.1. Burrows

Current scholarship generally supports a Devonian earliest occurrence of vertebrate burrowing (e.g., Benton, 1988; Hasiotis et al., 2007; Lucas, 2019) (Table 1).

The oldest potential vertebrate burrow is *Cornulatichnus edayensis* Carroll and Trewin, 1995. It was described from Scotland, from the Eday Marls and Upper Eday Sandstone (part of the Old Red Sandstone) and has a Givetian age. It is a conical structure with elliptical section, perpendicular to the substrate and tapering downwards, about 38–90 cm long and 4 cm wide. After a comparison with modern-day burrows, an eel-like fish has been proposed as a possible producer (Carroll and Trewin, 1995).

The oldest potential lungfish burrow has been described from the Old Red Sandstone of Ireland, and is dated Givetian-Fammenian (O'Sullivan

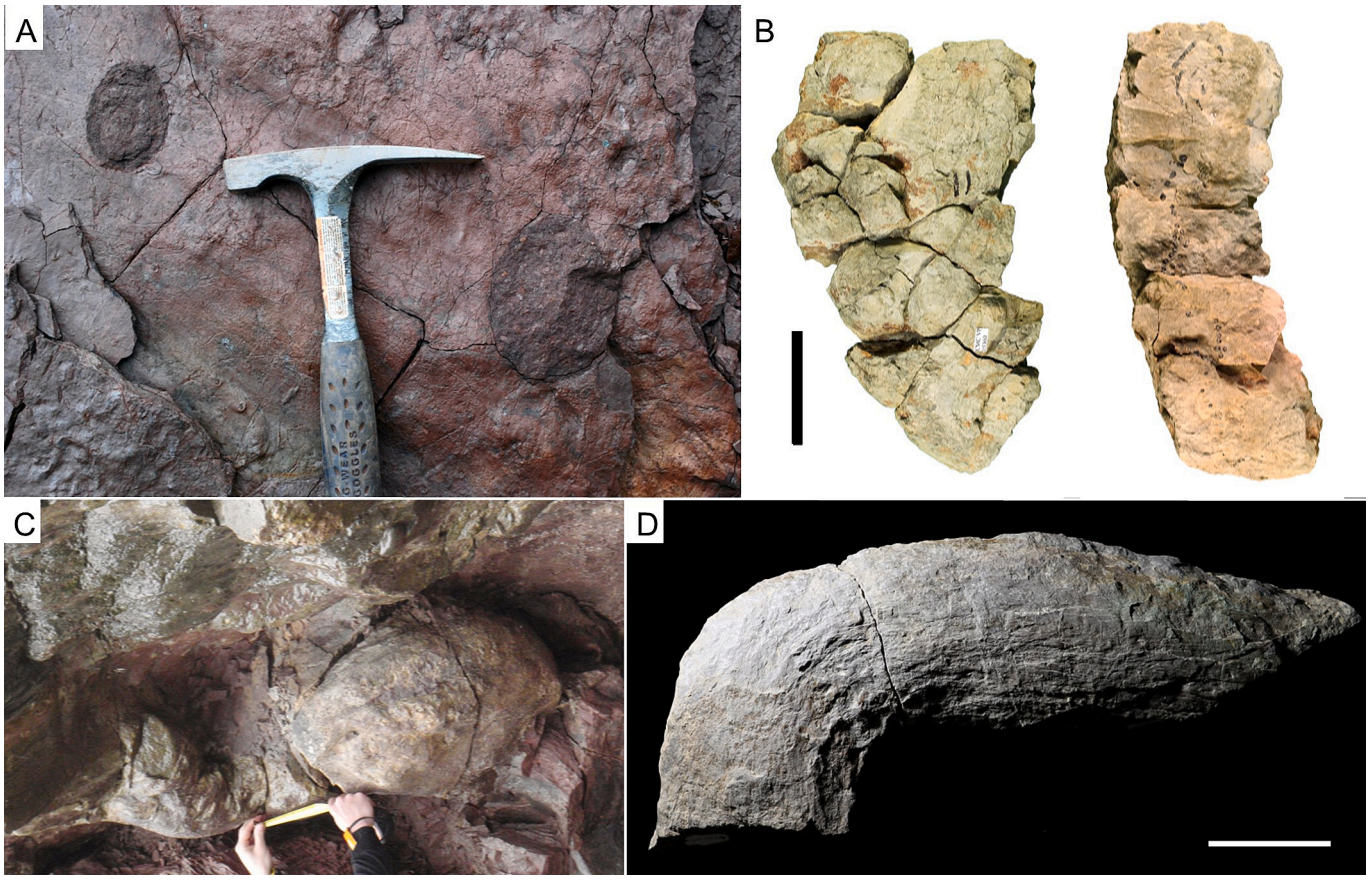

Fig. 9. Devonian and Carboniferous vertebrate burrows. A) Sub-vertical burrows of possible lungfish origin, horizontal sections, top view. Catskill Formation, Late Devonian, Pennsylvania. Photo courtesy of E.B. Daeschler. B) CMC VP15360. Sub-vertical burrow infill tapering downwards, with elliptical section. Views of the wider and narrower sides. It includes a lungfish skeleton, cf. *Tranodis*. Menard Limestone, Mississippian, Carboniferous, Kentucky. Scale bar = 5 cm. Photos courtesy of C. Schwalbach and G.W. Storrs. C) Low-angle burrow infill with sinusoidal tunnel and enlarged chamber at the mudstone/conglomerate transition, lateral view. Probable tetrapod origin. Mauch Chunk Formation, Mississippian, Carboniferous, Pennsylvania. Photo courtesy of S.G. Lucas. D) MNG-VF 2003. Low-angle curved burrow with scratch marks of tetrapod origin. Ilmenau Formation, Pennsylvanian, Germany. Scale bar = 5 cm.

et al., 1986). Two types of burrows were described, one discordant with stratification and about 4–8 cm wide in sandstones and a second at an angle of 5–10° with bedding, up to 2.3 m long and 6–18 cm wide and showing internal lamination, in siltstone. Both were considered to be passively infilled burrows without menisci and thus distinguished from *Taenidium barretti*. However, because of morphology, size, and internal structure, the second record is remarkably similar to *Taenidium barretti* from other units of the Old Red Sandstone (e.g., Allen and Williams, 1981). Lungfish burrows, subvertical, 5–8 cm wide with a circular or elliptical section, have also been reported from the Catskill Formation of Pennsylvania, dated as Fammenian, a unit that yields lungfish body fossils (e.g., Woodrow et al., 1973; Friedman and Daeschler, 2006) (Fig. 9A).

5.1.2. Potential producers

The only Devonian vertebrate taxa that have been ascribed a burrowing lifestyle are fishes, and in particular lungfishes (Sarcopterygii: Dipnoi), although none has yet been found preserved within a burrow (Friedman and Daeschler, 2006).

5.2. Carboniferous

5.2.1. Burrows

In the Carboniferous, although not common, lungfish burrows still occur (Table 1). Also, there is the first occurrence of a lungfish skeleton within a burrow, from the Mississippian (Namurian A) Menard Limestone of Kentucky (Horner and Storrs, 2002; Garcia et al., 2006). The burrow is about 20 cm deep, 10 cm wide, almost vertical and tapering downwards, with an irregular outer wall. The skeleton preserved within was assigned to the lungfish taxon cf. *Tranodis* (Garcia et al., 2006) (Fig. 9B). Further potential lungfish burrows have been described from the Pennsylvanian Breathitt Formation of Kentucky (Thomas and Blodgett, 1986) and Saginaw Group of Michigan (Carroll, 1965).

Moreover, the earliest potential tetrapod burrows are described from the Carboniferous (e.g., Voigt, 2005; Storm et al., 2010; Hembree et al., 2011) (Table 1), although this record is not extensive and the attribution to tetrapods is generally uncertain. The earliest putative tetrapod burrow is from the Mississippian Mauch Chunk Formation of Pennsylvania (Storm et al., 2010; Lucas, 2019) (Fig. 9C). This structure has a flared opening, a curved oblique tunnel of 15–20 cm in diameter and a wide, ovoid terminal chamber, 51–60 cm in diameter and about 20 cm high. Storm et al. (2010) hypothesized a tetrapod producer (more specifically an amphibian, because synapsids and reptiles appeared later in the Pennsylvanian).

Hembree et al. (2011) described complex burrow systems of either vertebrate or invertebrate origin from the Upper Pennsylvanian (Virgilian) Monongahela Group of Ohio (Table 1). These burrows developed on a horizontal plane in a mudstone and are filled in by a calcareous mudstone similar to the overlying unit, suggesting passive infill. They are constituted by a network of elliptical to circular, horizontal, branching tunnels of 1–18 cm in diameter, crossing with X, Y, and T

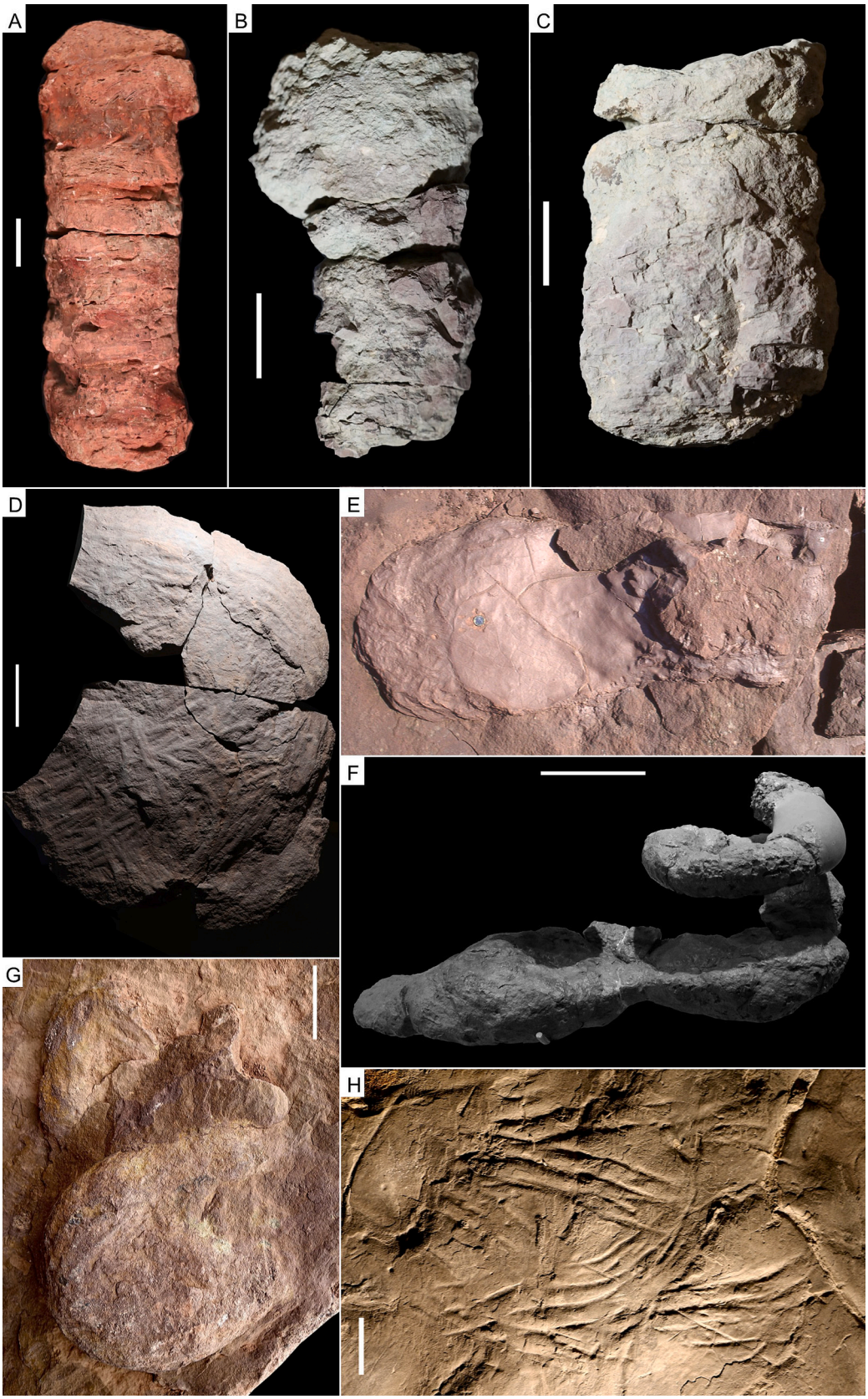

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Fig. 10. Permian vertebrate burrows. A-C) Sub-vertical burrow infills. A) FMNH-PF 12592. Burrow with circular section, lateral view. Possible lungfish producer. Vale Formation, Cisuralian, Texas. Scale bar = 2 cm. B—C) *Torridorefugium eskridgensis*. Speiser Shale, Cisuralian, Kansas. B) KU 138009. Holotype, burrow tapering downwards with elliptical section, view of the wider side. Scale bar = 2 cm. C) KU 138023. Burrow with elliptical section, view of the wider side. Scale bar = 2 cm. D—H) Low-angle burrows. D-E) Tambach Formation, Cisuralian, Germany. D) MNG-16850. Spiral burrow infill with scratch marks in convex hyporelief, bottom view. Scale bar = 10 cm. E) Sub-horizontal burrow infill termination with scratch marks on the sides in convex hyporelief, top-lateral view. Photo courtesy of T. Martens. F) SAM-PT-K10432. Spiral burrow infill ending in an enlarged chamber, lateral view. Teekloof Formation, Guadalupian, South Africa. Scale bar 10 cm. G-H) Lopingian, Germany. G) MfNMD P-22250. Burrow termination with scratch marks in convex hyporelief, bottom view. Scale bar 10 cm. H) MfNMD P-21652. Scratch trace sets in concave epirelief on a mudstone with mud cracks, top view. Scale bar 5 cm.

junctions. These have been interpreted as dwelling structures of animals living in freshwater environments, possibly crustaceans or small tetrapods. Lacking definite evidence of either hypothesis, the producer assignment is still uncertain.

Voigt (2005) described some potential tetrapod burrow infills from the Upper Pennsylvanian (Gzhelian) Ilmenau Formation of Germany (Fig. 9D) (Table 1). These are cylindrical, almost horizontal, straight or curved burrows up to 140 cm long and about 10 cm wide with scratch traces on the bottom and sides, preserved in sandstone layers.

5.2.2. Potential producers

During the Carboniferous, lungfish can be confidently stated to be capable of fossorial behaviour, with lungfish remains being found within what are considered aestivation burrows (Horner and Storrs, 2002; Garcia et al., 2006) (Fig. 9B) (Table 2). Some "lepospondyls" that appeared in the Carboniferous, and in particular phlegethontid aistopods, have been suggested to be fossorial because of their highly ossified braincase, forward position of the jaws, large, round stapedial footplate, and low neural spines (Gregory, 1948). However, this was questioned by Anderson (2002), who considered the presence of the posterior process and the large orbits and lightly built, fenestrate skull not compatible with fossorial habits but instead in agreement with a terrestrial lateral undulatory behaviour.

The most commonly suggested group of tetrapods capable of fossorial behaviour during the Carboniferous are recumbirostran "microsaurs" (Table 2). First appearing in the fossil record during the late Carboniferous, many recumbirostrans exhibit adaptations to their skulls and postcrania that could have allowed for a fossorial lifestyle. Their most notable fossorial feature being the recumbent snout for which the clade is named (Anderson et al., 2009), they exhibit various skull shapes that can be interpreted as adaptations for moving substrate (Mann and Maddin, 2019). Other potential fossorial features often found within the group are reduced limbs and elongated bodies (Maddin et al., 2011). For example, molgophid recumbirostrans have elongated bodies and reduced limbs, and due to these features members of the clade are generally considered to be fossorial (Bolt and Wassersug, 1975; Pardo and Anderson, 2016; Mann et al., 2019, 2021, 2022), probably soil-crawling. In contrast, there are recumbirostran clades appearing during the Carboniferous that contain members considered to be fossorial, but show different skeletal modifications, probably due to a different digging style, such as scratch-digging. For instance, the miniaturized brachystelechids exhibit a small fusiform body and well-developed limbs (Mann and Maddin, 2019).

Interestingly, some supposed tetrapod burrows from Carboniferous units (Voigt, 2005; Storm et al., 2010) are significantly larger than known aistopods and recumbirostrans of that time; therefore different producers can be hypothesized. In the late Mississippian only anamniotes are known, so the producer of large burrows of that age from Pennsylvania probably belongs to this group (Lucas, 2019). Conversely, in the Gzhelian, synapsids and reptiles also occurred, so the later burrows from Germany have a wider spectrum of potential producers (Voigt, 2005).

5.3. Permian

5.3.1. Burrows

Vertebrate burrowing becomes more common and complex in the Permian (Table 1). In the Cisuralian of North America, there is an abundant record of sub-vertical burrows interpreted as lungfish and recumbirostran "microsaur" aestivation structures, often in dense concentrations and sometimes in association with skeletal remains of the possible producers (e.g., Olson and Bolles, 1975; Hembree et al., 2004). Burrows attributed to lungfish in the Cisuralian are generally sub-vertical cylindrical structures with a cup- or flask-shaped base and a checker-like preservation (Figs. 4A, 10A), and some include lungfish remains assigned to *Gnathorhiza* (e.g., Olson and Bolles, 1975). They have been reported from the Arroyo, Vale, and Choza Formations of Texas (Romer and Olson, 1954; Dalquest and Carpenter, 1975; Olson and Bolles, 1975; Dalquest et al., 1989), the Wellington Formation and Hennessey Group of Oklahoma (Carlson, 1968; Olson and Bolles, 1975), the Speiser Shale and Matfield Shale of Kansas (Schultze, 1985; Cunningham and Dickson III, 1996; Hasiotis et al., 2002; McCahon and Miller, 2015), the Sangre de Cristo, Abo and Robledo Mountains formations of New Mexico (Vaughn, 1964; Berman, 1976; Voigt et al., 2013), and the Kildare Capes Formation of Prince Edward Island, Canada (Langston, 1963). A further occurrence of possible lungfish burrows is from the Guadalupian of the Rio do Rasto Formation of Brazil (Francischini et al., 2018).

Burrows attributed to recumbirostran "microsaurs" are generally conical structures, elliptical in section, that taper distally, and have been reported from the Cisuralian Choza Formation of Texas, Fairmont Shale of Oklahoma (Olson and Bolles, 1975), and Speiser Shale of Kansas (Schultze, 1985; Cunningham and Dickson III, 1996; Hembree et al., 2004). These burrows sometimes contain remains of "microsaurs", and specifically Molgophidae such as *Brachydectes* (formerly assigned to the dubious genus *Lysorophus*) (e.g., Olson and Bolles, 1975; Hembree et al., 2004). Hembree et al. (2005) provided a detailed description of burrows from the Speiser Shale of Kansas and introduced the ichnotaxon *Torridorefugium eskridgensis* (Fig. 10B-C).

Relatively large tetrapod burrows associated with sets of scratch traces are found in the Cisuralian of North America (Maroon Formation of Colorado; Voigt et al., 2021) and Europe, some with a spiral pattern (Tambach Formation of Germany; Martens, 2001a, 2001b, 2005; Herde et al., 2022; Marchetti et al., 2022a) (Figs. 4H-I, 10D-E). Nevertheless, it is only at the end of Guadalupian and in the Lopingian that tetrapod burrowing structures become more abundant and complex (e.g., Smith, 1987; Lagnaoui et al., 2015). Smith (1987) and Smith et al. (2021) described several helical and horizontal declining tetrapod burrows from the Capitanian-Wuchiapingian transition of the Karoo Basin in South Africa. The helical burrows (Fig. 10F) have been assigned by Smith et al. (2021) to cf. *Daimonelix*, although notable differences from the typical Cenozoic *Daimonelix* produced by castorid rodents can be observed. These include, for instance, the spiral diameter increasing downward and the lower ramp angle. Smith et al. (2021) assigned the declining burrows to cf. *Reniformichnus*, although the section is elliptical and not kidney-shaped. In three chambers, articulated *Diictodon* skeletons have been found (Smith, 1987). The declining burrows yielded disarticulated remains of adult and infant *Diictodon* (Smith et al., 2021).

Buchwitz et al. (2018) reported scrambling traces from the Guadalupian-Lopingian Mammendorf locality of Germany (Fig. 10G-H). Some of these traces are parts of burrows (Fig. 10G) and a possible medial ridge can be observed. These structures have been attributed to therapsids, also because of their association with *Dicynodontipus* footprints.

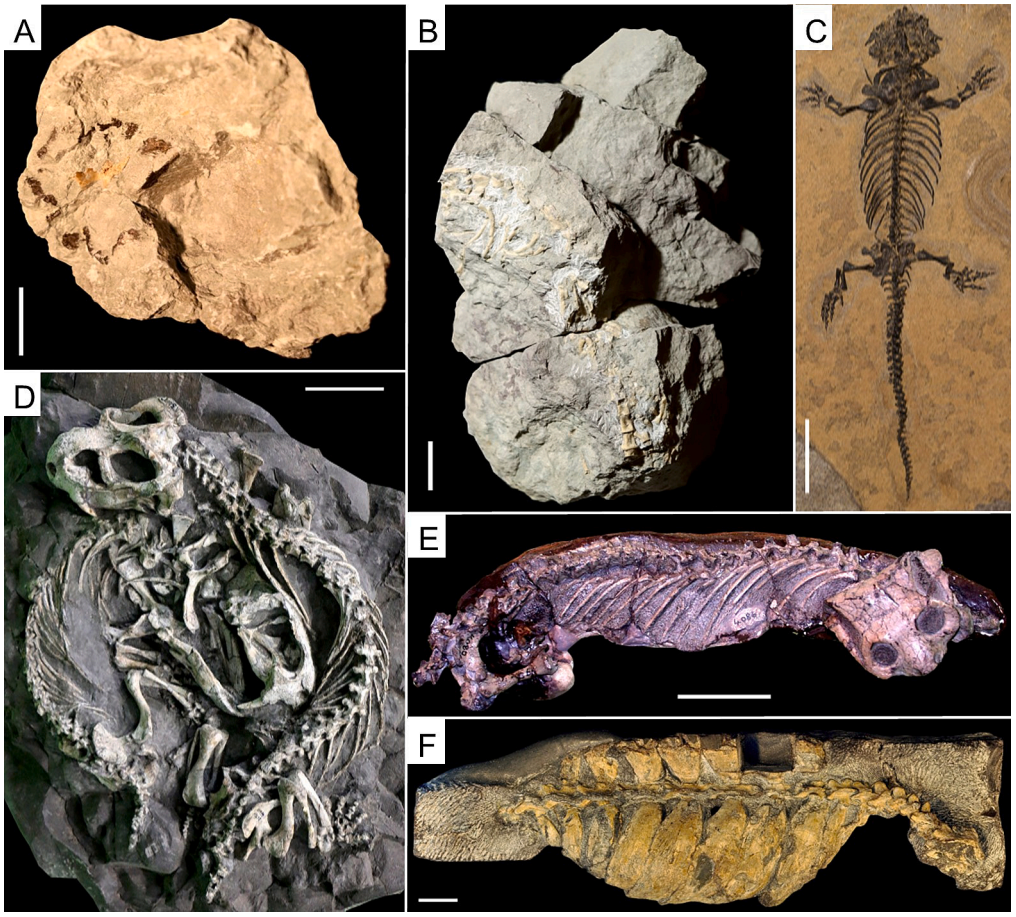

Fig. 11. Permian fossorial vertebrates. A) KU-NN 1. Lungfish tooth in a sub-vertical horizontal burrow section, top view. Scale bar = 1 cm. Speiser Shale, Cisuralian, Kansas. B—C) Recumbirostra. B) KU 138002. *Brachydectes elongatus* skeleton in a sub-vertical burrow tapering downwards, view of the wider burrow side. Scale bar = 1 cm. Speiser Shale, Cisuralian, Kansas. C) MNHM PW 2001/307-LS. *Batropetes palatinus*, dorsal view. Scale bar = 1 cm. Meisenheim Formation, Cisuralian, Germany. D-E) Therapsida. D) SAM-PK-K5477. *Diictodon feliceps*, two individuals, dorsal view. Guadalupian, South Africa. Scale bar = 5 cm. E) BP/1/4086. *Cistecephalus microrhinus*, dorsal-lateral view. Lopingian, South Africa. Scale bar = 5 cm. F) CM 86–341. Diapsida, *Eunotosaurus africanus*, dorsal view. Guadalupian, South Africa. Scale bar = 1 cm. Photo courtesy of T.R. Lyson.

Further burrows attributed to amniotes are reported from the Guadalupian-Lopingian Ikakern Formation of Morocco, which are potentially communal structures (Lagnaoui et al., 2015), the Naobaogou Formation of China (Liu and Li, 2013), and the Lopingian-Induan Buena Vista Formation of Brazil, which are burrows from aeolian palaeoenvironments (Francischini et al., 2023).

Voigt (2005) reported on a poorly-preserved sub-circular structure from the lower Cisuralian Goldlauter Formation of Germany. Because of the elevated ridges, this has been interpreted as a superficial nest structure.

5.3.2. *Potential producers*

During the Permian there are numerous tetrapod taxa that have been ascribed a burrowing lifestyle; it is during this period that we start to see a wider array of groups exhibiting morphologies that suggest fossoriality (Table 2).

Lungfish remains such as *Gnathorhiza* are found in burrows, suggesting fossorial habits (Fig. 11A) (e.g., Dalquest et al., 1989). The skeletons of *Gnathorhiza* from the lower Permian Arroyo Formation of Texas are either disarticulated or in life position, with the tail oriented towards the bottom of the burrow; they can also show mummified skin, the result of desiccation (Dalquest et al., 1989).

Following their first appearance in the late Carboniferous, recumbirostran "microsaurs" (Fig. 11B-C) continued to diversify into the Permian, though the clade goes extinct by the end of the Cisuralian. All of the recumbirostran clades that exhibited potential burrowing taxa during the Carboniferous are still present in the early Permian, with several taxa having potential adaptations for fossoriality, including brachystelechids (Maddin et al., 2011; Glienke, 2015; Pardo et al., 2015; Jansen and Marjanović, 2022) (Figs. 7E, 11C), molgophids (Bolt and Wassersug, 1975), hapsidopareiids (Gee et al., 2019), ostodolepidids (Anderson et al., 2009; Henrici et al., 2011; MacDougall et al., 2021) (Fig. 7C), as well as various others (Huttenlocker et al., 2013; Szostakiwskyj et al., 2015). Furthermore, coiled skeletons of presumed adult *Brachydectes* (centra length 10.5–13.5 mm) have been found within vertical burrows from the Choza Formation of Texas and Fairmont Shale of Oklahoma (Olson and Bolles, 1975), as well as the Speiser Shale of Kansas (Olson and Bolles, 1975; Hembree et al., 2004; Hembree et al., 2005) (Fig. 11B). Smaller *Brachydectes* skeletons (centra length 2.5–10.0 mm) have also been found preserved coiled in ovoid nodules in the Arroyo, Vale, and Choza formations of Texas and the Fairmont Shale of Oklahoma, and been interpreted as resulting from aestivation in a burrow (Olson and Bolles, 1975).

Remains assigned to the "lepospondyl" *Diplocaulus* have been found within a burrow in the Cisuralian Speiser Shale of Kansas (Cunningham and Dickson III, 1996), but it is unclear if this animal could have been fossorial. Curled-up skeletons of *Diplocaulus* and the temnospondyl *Eryops* from the Cisuralian of Texas have been interpreted as animals that died during aestivation (Zoehfeld et al., 2013).

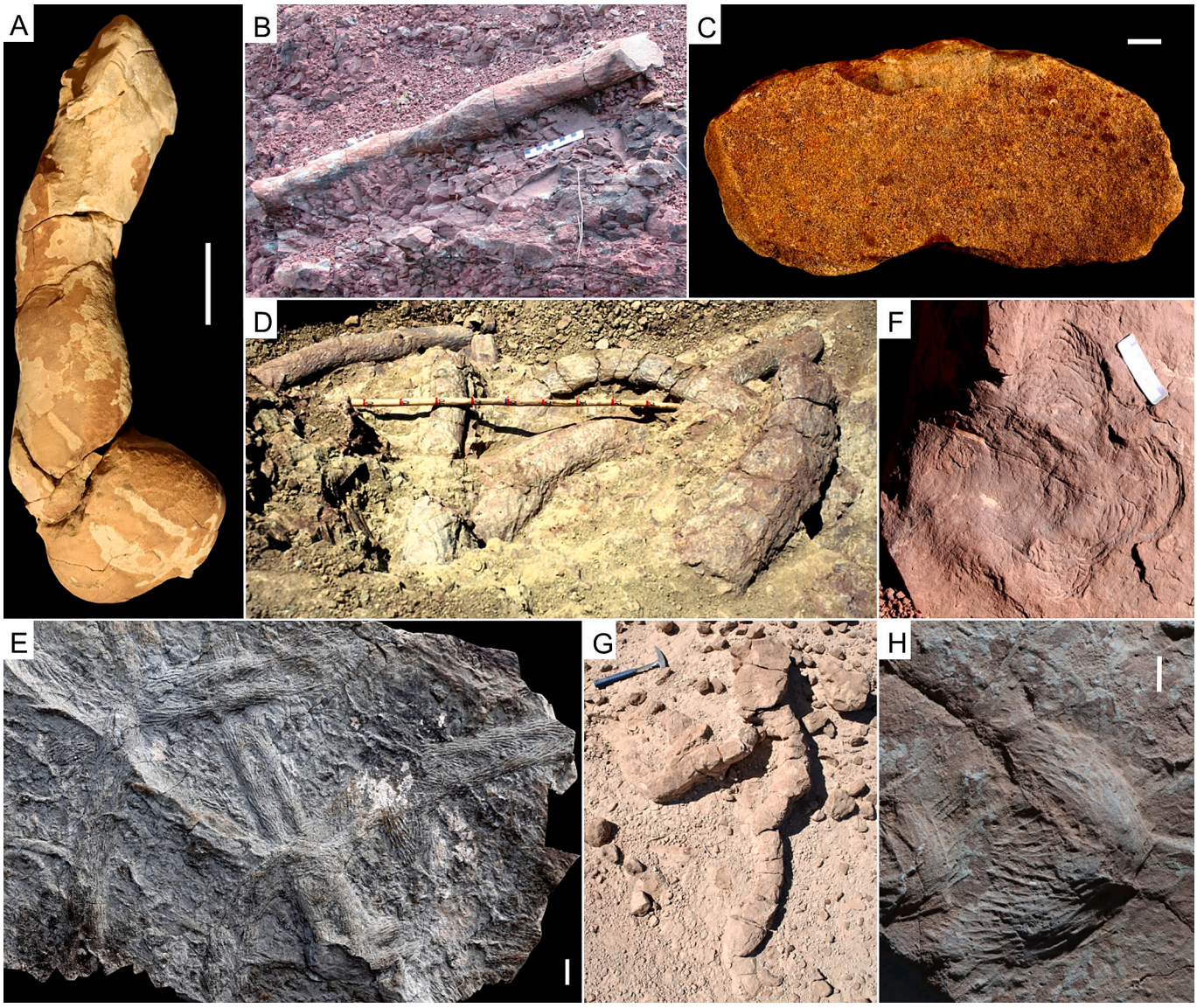

Fig. 12. Triassic vertebrate burrows. A) NMMNH P-50409. *Redondarefugium abercrombieorum*, holotype. Sub-vertical burrow, potential lungfish producer, lateral view. Redonda Formation, Late Triassic, New Mexico. Scale bar = 5 cm. B—H) Low-angle burrows. B—C) BP/6/698. *Reniformichnus katikatii*, holotype. Katberg Formation, Early Triassic, South Africa. Photos courtesy of E.M. Bordy. B) Lateral view of the burrow infill. C) Kidney-shaped burrow section. Scale bar = 1 cm. D) Complex burrow infill preserved in mudstone. Burgersdorp Formation, Early Triassic, South Africa, lateral view. Photo courtesy of G.H. Groenewald. E) Base of a complex burrow system showing parallel rows of scratch trace sets in convex hyporelief in sandstone, bottom view. Burgersdorp Formation, Middle Triassic, South Africa. Scale bar = 10 cm. F) Terminal chamber roof with multiple lobes and scratch traces preserved in sandstone, concave epirelief, bottom view. Timezgadiouine Formation, Middle Triassic, Morocco. Photo courtesy of H. Saber. G) Complex burrow infill. Chañares Formation, Late Triassic, Argentina. Photo courtesy of L.E. Fiorelli. H) Scratch trace sets at the base of a tunnel termination, convex hyporelief, bottom view. YPM 8264. Blomidon Formation, Late Triassic, Nova Scotia. Scale bar = 1 cm.

Large-sized tetrapod burrows described from the Cisuralian of Germany and Colorado do not have definite producers, but indicate the presence of substantially larger fossorial taxa than the recumbirostran "microsaurs" of the same time interval (Martens, 2005; Voigt, 2005; Herde et al., 2022).

First appearing during the Guadalupian is the synapsid clade Dicynodontia (Fig. 11D-E), which soon thereafter became an important and common component of terrestrial ecosystems. Many Permian members of this clade have been suggested to be fossorial by various workers. All members of the clade Cistecephalidae are considered to be fossorial due to numerous modifications to their skulls and postcrania (e.g., Cox, 1972; Cluver, 1974; Kammerer et al., 2016; Angielczyk et al., 2019) (Figs. 7A-B, 11E). Other possibly fossorial dicynodonts include *Diictodon* (Fig. 11D), which has been found within helical or straight burrow structures from the Capitanian-Wuchiapingian of the Karoo Basin in South Africa (Smith, 1987; Smith et al., 2021). Other *Diictodon* skeletal material has been found that is not within a discernible burrow cast, but which shows a peculiar "coiled" preservation at an angle consistent with the helical burrow structures (Smith, 1987). The termination of one of the straight burrow infills yielded a disarticulated adult *Diictodon* skeleton and the humerus of an infant *Diictodon*. Since the disarticulation is moderate, it has been interpreted as skeletons originally within a burrow moved by a relatively slow current that filled it in. Therefore, they would constitute possible evidence of breeding behaviour within the burrow. Additionally, a specimen with the association of an adult *Diictodon* overlaying two infant *Diictodon* and underlaying a therocephalian

(*Ictidosuchoides*) skeleton has been interpreted as consistent with preservation in a burrow (Smith et al., 2021). The larger late Permian dicynodont *Oudenodon* has also been considered potentially fossorial, due to the thick cortical walls of its long bones (Botha, 2003).

The diapsid reptile *Eunotosaurus* appears in the fossil record during the Guadalupian and is considered to be fossorial due to its dramatically broadened ribs, which would have acted as a sturdy base to support muscle attachment, facilitating powerful digging motions by the forelimbs (Lyson et al., 2016) (Fig. 11F).

5.4. Triassic

5.4.1. Burrows

During the Triassic, cylindrical, sub-vertical burrows attributed to lungfish aestivation are reported (Table 1), and are especially abundant in the Late Triassic of the USA, where they are sometimes found in high concentrations (e.g., Dubiel et al., 1987; Lucas et al., 2010). Dubiel et al. (1987) described supposed lungfish aestivation burrows from the Upper Triassic Chinle Formation of Utah, Arizona, and New Mexico and the Upper Triassic Dolores Formation of Colorado, although the attribution to lungfish has been questioned because of the absence of associated skeletons (McAllister, 1988). Gobetz et al. (2006) and Lucas et al. (2010) described further material from the Upper Triassic Redonda Formation of New Mexico. Elongated cylindrical structures, 4.8–7.2 cm in diameter, vertical or inclined, slightly helical, with no surface structures except for wrinkles, weathering in checker-like shapes and ending in enlarged chambers thus forming flank-like shapes, have been assigned to the new ichnotaxon *Redondarefugium abercrombieorum* Lucas et al., 2010 (Fig. 12A). Further sub-vertical cylindrical burrows related to lungfish aestivation have been described from Lower and Middle Triassic units of Russia (Sennikov, 2018) and the Lower Triassic Katberg Formation of South Africa (Bordy and Krummeck, 2016).

Triassic burrows attributed to tetrapods are relatively common and seem to be particularly abundant in the aftermath of the terrestrial end-Permian extinction (e.g., Miller et al., 2001; Modesto and Botha-Brink, 2010; McLoughlin et al., 2020) (Table 1).

Some burrows from a unit around the P-Tr boundary, the Palingkloof Member of the Balfour Formation (South Africa), include articulated skeletal remains, such the cynodont *Thrinaxodon liorhinus* (Damiani et al., 2003) and the dicynodont *Lystrosaurus curvatus* (Botha-Brink, 2017), and some disarticulated remains, such as *Lystrosaurus* sp. (Modesto and Botha-Brink, 2010). Co-existence of different species and even clades within a burrow has been described by Fernandez et al. (2013), in a specimen from the Harrismith Member of the Normandien Formation of South Africa (*Lystrosaurus declivis* Assemblage Zone - AZ). The burrow infill is a silty fine-grained sandstone, 96–150 mm in diameter. It includes a fully-articulated skeleton of the cynodont *Thrinaxodon liorhinus* and the temnospondyl *Broomistega putterilli*.

Krummeck and Bordy (2018) introduced the ichnotaxon *Reniformichnus katikatii* for tetrapod burrows from the Lower Triassic Katberg Formation of South Africa (Figs. 4D, 12B-C). It is characterised by unbranched, isolated, straight to gently sinusoidal tunnels inclined up to 30° with a characteristic kidney-shape section produced by two distinct grooves into the burrow floor. The width ranges from 12.6 to 14.7 cm and the height from 5.0 to 7.4 cm. The outer wall is covered by scratch traces parallel to the direction of the tunnel. The infill of siltstone or sandstone is passive and coarser than the embedding mudstone. Additional burrows attributed to tetrapods from the same formation have been described by Bordy et al. (2009, 2011) (Fig. 4F). Groenewald (1991) described four burrow morphotypes attributed to tetrapods from the Balfour and Katberg formations of South Africa, with burrow type 1 being provisionally re-assigned to *Reniformichnus* by Krummeck and Bordy (2018). Groenewald (1991) also reported skeletal material of dicynodonts and procolophonids from the described burrows.

The Triassic is characterised by the first definitive appearance of complex tetrapod burrows, indicating communal behaviour (Groenewald et al., 2001). A complex tetrapod burrow system has been described by Groenewald et al. (2001), from the Lower Triassic part of the Burgersdorp Formation (originally Driekoppen Formation, which has since been subsumed under the Burgersdorp; see Hancox et al., 2020) of South Africa (Figs. 4C, 12D). It includes straight to curved, sub-horizontal tunnels with an inclination of 1–23° that taper distally and end in a flattened terminus. The tunnel width is 6.3–15.4 cm and the tunnel height is 1.1–6.4 cm. The burrow section is kidney-shaped, but the floor of the terminal part is flat. Scratch traces are preserved on the outer walls. These burrows include cynodont skeletal remains, first assigned to *Trirachodon* and later to *Langbergia* (Groenewald et al., 2001; Abdala et al., 2006a, 2006b). Complex tetrapod burrows preserved on the bottom of a sandstone layer have been also described from the Middle Triassic part of the Burgersdorp Formation of South Africa (Bordy and Sciscio, 2017; Bordy et al., 2019; Figs. 6E, 12E). Further tetrapod burrows from the same unit have been described by Wolvaardt (2021), including a chamber with an articulated therocephalian, *Microgomphodon*.

Further tetrapod burrow occurrences in the aftermath of the end-Permian extinction have been described from Antarctica and Australia (e.g., Miller et al., 2001; McLoughlin et al., 2020). McLoughlin et al. (2020) described potential cynodont burrows from the basal Dooralong Shale of Australia, in the so-called “dead zone” immediately following the end-Permian extinction event. They were assigned to the new ichnospecies *Reniformichnus australis* McLoughlin et al., 2020. Three different burrow types attributed to tetrapods have been described from the Lower Triassic Fremouw Formation of Antarctica (Hasiotis et al., 1999, 2004; Miller et al., 2001; Sidor et al., 2008). Type G burrows of Miller et al. (2001) and “tetrapod ichnogenus A" of Sidor et al. (2008) were re-assigned to *Reniformichnus* isp. by Krummeck and Bordy (2018). Sidor et al. (2008) described further burrow structures (“tetrapod ichnogenus B") from the Middle Triassic Member A of the Lashly Formation of Antarctica.

Complex tetrapod burrows are relatively common throughout the Triassic (e.g., Voigt et al., 2011; Colombi et al., 2012; Fiorelli et al., 2018). Voigt et al. (2011) described complex burrows attributed to tetrapods from the Middle Triassic Timezgadiouine Formation of Morocco (Figs. 4E, G, 12F). They include oval entrances, elongated straight to sinuous tunnels with 10–30° of inclination, and can show Y-branching and widened multi-lobed chambers at the tunnel termination. Fiorelli et al. (2018) described complex tetrapod burrows from the basal Chañares Formation of Argentina, at the Middle-Upper Triassic transition (Figs. 4B, 12G). These structures are up to 6 m long and develop for areas of up to 17 m^2, reaching a depth of 1.6 m. After sub-vertical entrances, the tunnels develop sub-horizontally (5–30° in inclination), are sinuous, commonly showing Y-branches of 90–120°. Colombi et al. (2008, 2012) described complex tetrapod burrows from the Upper Triassic Ischigualasto Formation of Argentina (“Morphotype 1”). These burrows are sub-horizontal tunnels with short vertical shafts covering areas of up to 2 square metres. Tunnels show relatively frequent T-branching. The tunnels can end in enlarged flattened chambers of up to 25 cm in diameter. Colombi et al. (2008, 2012) also described a burrow system (“Morphotype 2”) from the overlying Los Colorados Formation (Upper Triassic) made up of one or two, intersecting, sub-horizontal, straight tunnels with elliptical section and flat to wavy base.

Ellenberger (1976) described a supposed partial hairy therapsid track from the Middle Triassic of Lodève, France and named it *Cynodontipus polythrix*. A similar specimen from the Middle Triassic Buntsandstein/Muschelkalk transition of Germany was also assigned to this ichnotaxon. Sues and Olsen (2015) considered this ichnotaxon to be the bottom of a tetrapod burrow with scratch traces, probably produced by an amniote. Sues and Olsen (2015) described similar structures (about 5–10 cm wide) from the Upper Triassic Blomidon Formation of Nova Scotia (Fig. 12H).

Sub-horizontal burrows ending in oval terminal chambers attributed to tetrapods, possibly cynodonts, have been described from the Middle

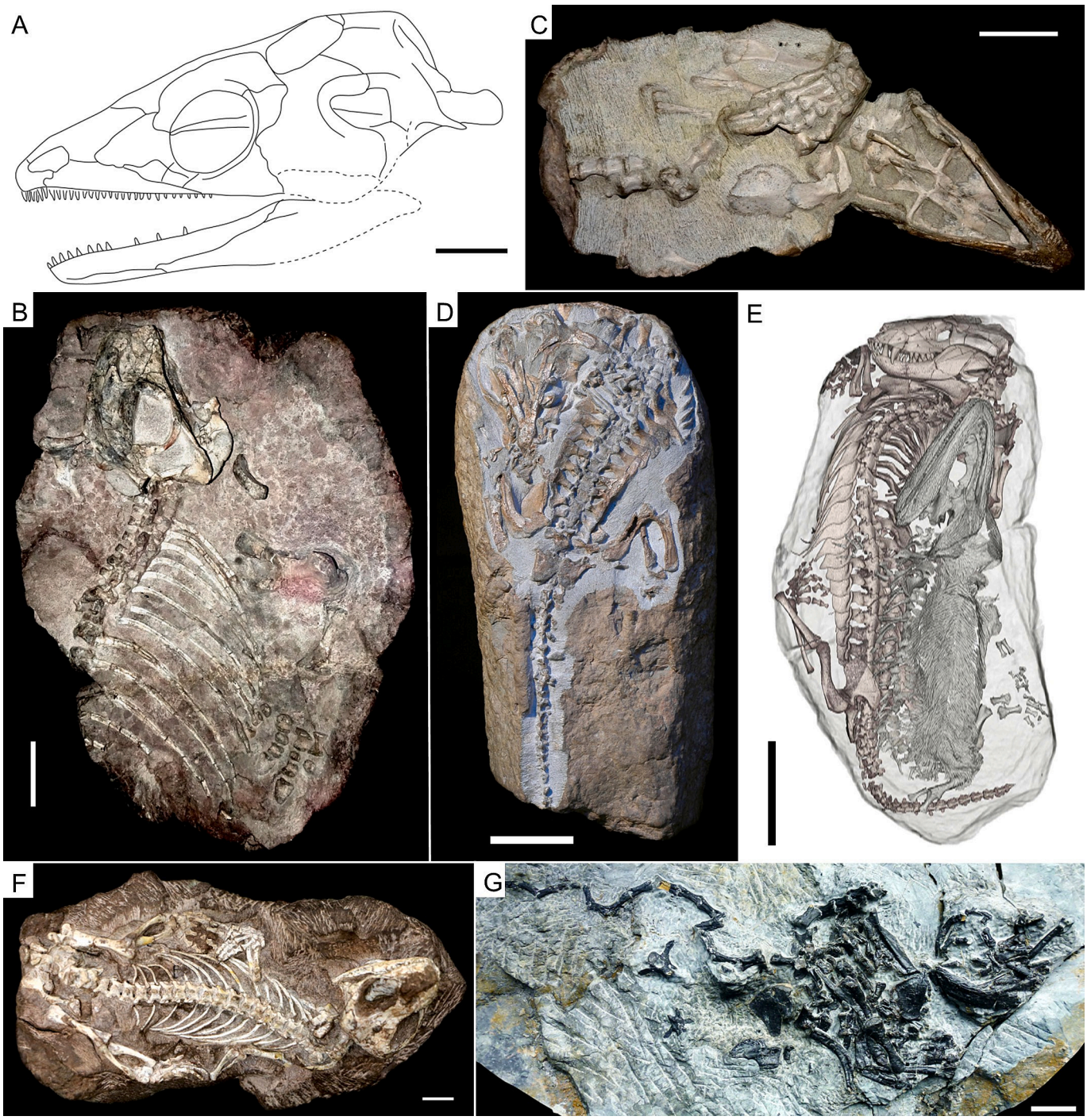

Fig. 13. Triassic fossorial vertebrates. A) Temnospondyli. *Chinlestegophis jenkinsi*, skull reconstruction, lateral view. Chinle Formation, Colorado, Late Triassic. Scale bar = 5 mm. Redrawn from Pardo et al. (2017). B-E) Therapsida. B) NMQR 4001. *Lystrosaurus curvatus* in a burrow infill, dorsal view. Scale bar 5 cm. Balfour Formation, Permian-Triassic transition, South Africa. C) AM 3677. *Tetracynodon darti*, ventral view with manus in dorsal view. Katberg Formation, Early Triassic, South Africa. Scale bar = 2 cm D) BP/1/5905. *Thrinaxodon liorhinus* in a burrow infill, dorsal view. Balfour Formation, Permian-Triassic transition, South Africa. Scale bar = 5 cm. Photo courtesy of C.A. Sidor. E) BP/1/5558, burrow cast. 3D rendering in semi-transparency showing *Thrinaxodon liorhinus* (in brown) and the temnospondyl *Broomistega putterilli* (in grey). Normandien Formation, Early Triassic, South Africa. Scale bar = 5 cm. Image courtesy of V. Fernandez. F) NMQR 3602. Procolophonidae. *Sauropareion anoplus*, dorsal view. Katberg Formation, Early Triassic, South Africa. Scale bar = 1 cm. G) SMNS 91360. Diapsida. *Pappochelys rosinae*, holotype, dorsal view. Erfurt Formation, Middle Triassic, Germany. Scale bar = 1 cm. Photo courtesy of R. Schoch. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Triassic Otter Sandstone Formation of England (Gallois, 2013), Tarjados Formation of Argentina (Krapovickas et al., 2013), and from the Upper Triassic Keuper of Poland (Tałanda et al., 2011).

Structures interpreted as superficial digging related to nesting have been described from the Upper Triassic Owl Rock Member of the Chinle Formation of Arizona (Hasiotis et al., 2004) and the Monticello Formation of Italy (Avanzini et al., 2007). The latter are circular-to-horseshoe-shaped depressions of 100–160 cm in maximum diameter. They are 5–20 cm deep and surrounded by rims. Archosaurian producers have been suggested.

5.4.2. Potential producers

Lungfishes have not been found within Triassic burrows. However, the morphology of several sub-vertical Triassic burrows is consistent with a lungfish producer (e.g., Lucas et al., 2010).

The temnospondyl *Broomistega* has been found within a burrow from the Early Triassic of South Africa (Fernandez et al., 2013), however it is unlikely to have been the producer. The temnospondyl *Chinlestegophis jenkinsi* from the Upper Triassic Chinle Formation of Colorado (Fig. 13A) shows morphological features in agreement with fossoriality, and has been found within a burrow (Pardo et al., 2017) (Table 2). This is suggestive of a fossorial lifestyle, though it cannot be confirmed if it was a secondary occupant of the burrow or the burrow maker itself (Pardo et al., 2017). The temnospondyl *Funcusvermis gilmorei* from the Upper Triassic Chinle Formation of Arizona was considered the earliest stem-caecilian in Kligman et al. (2023) (Table 2). It is worth noting that the morphologically similar modern caecilians are capable head-first burrowers (Hildebrand, 1974; Maddin et al., 2012).

The synapsid clade Dicynodontia passed through the end-Permian mass extinction event, with a few lineages surviving. One of these surviving lineages, the clade Lystrosauridae, contains the extremely abundant taxon *Lystrosaurus*, which has been suggested to be fossorial based on bone microstructure (e.g., Botha, 2020) and because specimens have been recovered from Triassic-aged burrow structures (Groenewald, 1991; Retallack et al., 2003; Botha-Brink, 2017) (Fig. 13B) (Table 2). Modesto and Botha-Brink (2010) described a burrow embedding a disarticulated *Lystrosaurus* specimen from the Palingkloof Member of the Balfour Formation. Because of disarticulation, smaller size of the skeleton compared to the burrow, and simplicity of the burrow structure, these authors proposed that the *Lystrosaurus* was prey and the burrower was its predator. Subsequent studies instead supported *Lystrosaurus* as the producer of this burrow (e.g., Bordy et al., 2011; Botha-Brink, 2017). Botha-Brink (2017) described a burrow chamber from the Palingkloof Member of the Balfour Formation embedding an articulated skeleton of *Lystrosaurus curvatus* (Fig. 13B). Mottling and discoloration have been observed around the skeleton and interpreted as possible decomposition effects. The articulated skeleton is the anterior part of a juvenile and includes an articulated right forelimb, ribcage, and skull in a dorsal-up position along the burrow axis, supporting interpretation as the burrow producer. Moreover, Botha-Brink (2017) highlighted how burrows may have favored both the survival of species across the P-Tr boundary and the preservation of their skeletons.

The baurioid therocephalian *Tetracynodon* has been suggested to be fossorial due to its large manus, short non-terminal phalanges, and long unguals (Fontanarrosa et al., 2019) (Figs. 7F, 13C) (Table 2). The bauriid therocephalian *Bauria* has been found in a burrow structure attributed to trirachodontid cynodonts, suggesting it may have opportunistically inhabited the burrow (Groenewald et al., 2001). However, Wolvaardt (2021) described the skeleton of another bauriid, *Microgomphodon*, in a

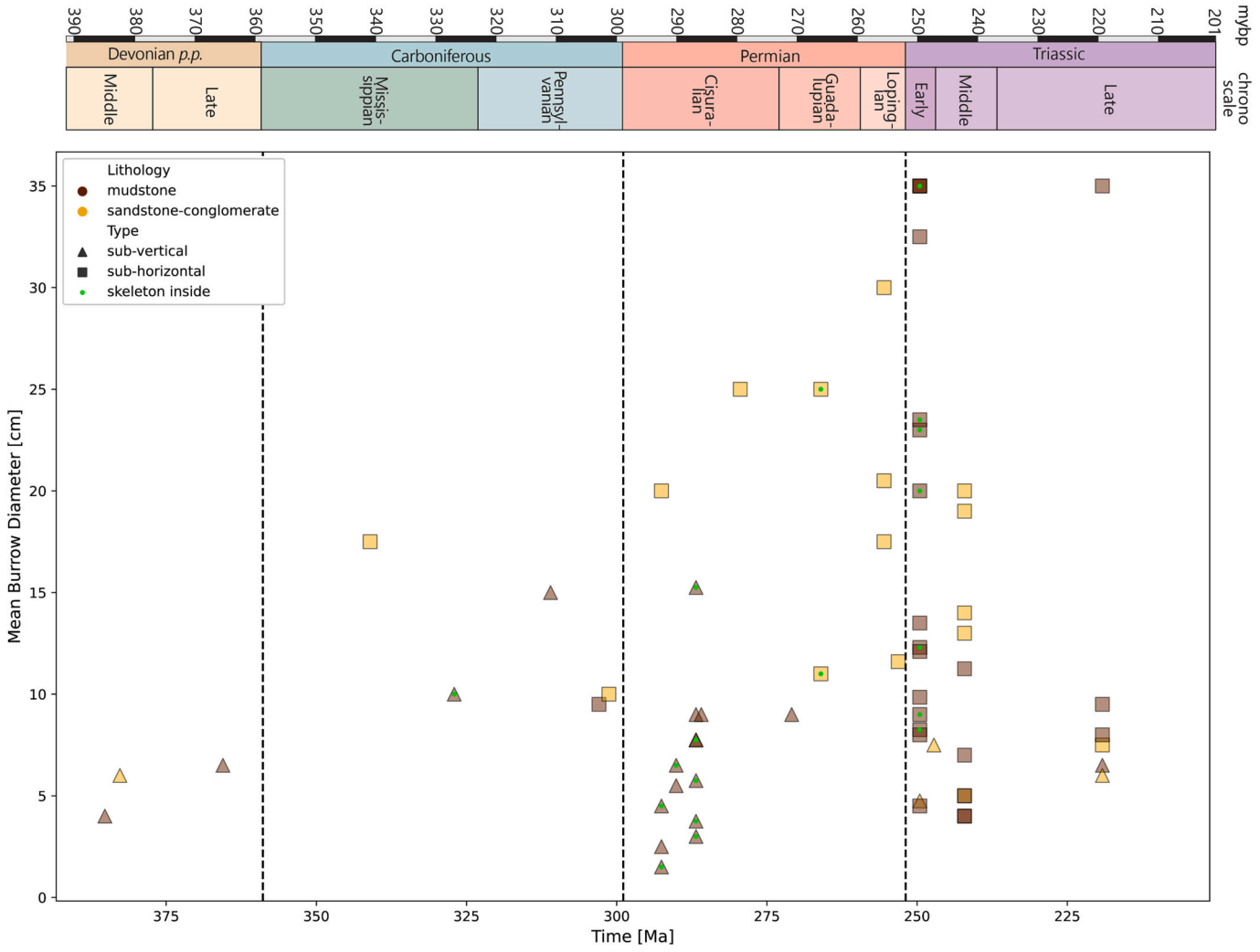

Fig. 14. Vertebrate burrow average diameter from Devonian to Triassic.

burrow terminal chamber from the Lower-Middle Triassic Burgersdorp Formation of South Africa, raising the possibility that bauriids were themselves burrow makers.

Other therapsids that have been attributed fossorial behaviour include the cynodonts *Trirachodon* (Botha and Chinsamy, 2004) and *Thrinaxodon* (Damiani et al., 2003; Botha and Chinsamy, 2005) in the Early Triassic, *Andescynodon* (Chinsamy and Abdala, 2008) in the Middle Triassic, and *Massetognathus* and *Probainognathus* in the Late Triassic (Garcia Marsà et al., 2022) (Table 2). All these taxa have been considered to be fossorial based on their bone microstructure, exhibiting thick cortical bone walls in their long bones (e.g., Chinsamy and Abdala, 2008). The Early Triassic cynodont *Galesaurus* has also been considered fossorial based on its postcranial features (Butler et al., 2018). Groenewald et al. (2001) described complex burrows from the Lower Triassic part of the Burgersdorp Formation of South Africa (Figs. 4C, 12D), including at least 20 different skeletons of a gomphodont cynodont (initially identified as *Trirachodon*, later assigned to a different trirachodontid taxon, *Langbergia*; Abdala et al., 2006a, 2006b), mostly in the terminal part of tunnels, in a curled position facing the burrow entrance. Therefore, this cynodont was suggested to be the producer of the burrow system (Table 2). Damiani et al. (2003) described a burrow cast embedding an articulated cynodont, *Thrinaxodon liorhinus*, from the Palingkloof Member of the Balfour Formation (Fig. 13D). Because of the skeleton's size, orientation, and limited disarticulation, *Thrinaxodon* was proposed as the burrow producer, exsiccated and not exposed for long before the flooding. Additional evidence of *Thrinaxodon* burrowing comes from a specimen described by Fernandez et al. (2013) from the Harrismith Member of the Normandien Formation of South Africa (*Lystrosaurus declivis* AZ). CT scanning of this burrow cast (Fig. 13E) revealed a complete articulated skeleton of *Thrinaxodon liorhinus* preserved dorsal side-up, associated with a complete articulated skeleton of the temnospondyl *Broomistega putterilli* preserved ventral side-up overlaying it. Three different infill layers have been identified, and both skeletons occupy the middle one. Fernandez et al. (2013) hypothesized that the most likely explanation was limited transport because of the low flood energy (causing the amphibian to flip but not disarticulate) and so suggested occupation of both forms during life, possibly the cynodont aestivating and the amphibian taking shelter because of injury. Abdala et al. (2006a, 2006b) also hypothesized simultaneous occupation of a burrow to interpret the co-occurrence of articulated skeletons, including delicate parts, in a side-by-side position. This association includes a skeleton of the cynodont *Galesaurus planiceps*, two individuals of the procolophonoid *Owenetta kitchingorum*, and a millipede. Both of these fossil finds are consistent with the hypothesis of shelter sharing by different taxa and thus with burrowing as an ecosystem engineering process, although the complexity of the potential associated burrow systems is unknown.

The procolophonid reptiles *Procolophon, Sauropareion*, and *Teratophon* have all been interpreted as fossorial based on the stout morphology of the forelimbs and on the bone microstructure, histological analysis revealing thickened cortical walls in their long bones (Botha-Brink and Smith, 2012) (Figs. 7D, 13F) (Table 2). Some procolophonids have been found within burrows or in the same stratigraphic horizons as similar-sized burrows (Groenewald, 1991; Sidor et al., 2008).

The diapsid reptile *Pappochelys rosinae* from the Middle Triassic of Germany (Fig. 13G), one of the earliest taxa in the turtle lineage, is another tetrapod from this period that has recently been considered fossorial due to histological data (Schoch et al., 2019) (Table 2). The microanatomy of the skeleton of *Pappochelys* provides evidence that supports a fossorial mode of life and suggests that the turtle shell evolved in a terrestrial environment, rather than an aquatic one (Schoch et al., 2019). Although most nominal species of the diapsid reptile clade Drepanosauromorpha have been considered arboreal, the taxa *Ancistronychus paradoxus* and *Skybalonyx skapter* from the Upper Triassic Chinle Formation of the southwestern USA have been suggested to have been fossorial based on discriminant function analysis on manual unguals III compared to modern taxa (Jenkins et al., 2020). The Late Triassic aetosaurian archosaur *Stagonolepis olenkae* from Poland has been considered a scratch-digger by Dróżdż (2018), based on the morphology of the forelimb, manus and unguals.

6. Discussion

6.1. Early evolution of vertebrate burrow structure

During the period spanning from the Devonian to the Triassic, vertebrate burrows show a significant change in size, structural complexity, and lithology of the host rock (Fig. 14, Table 1).

The earliest supposed vertebrate burrows (Devonian-Carboniferous) are simple, sub-vertical structures with biconvex (subcircular) section. Their diameter is on average 4.5–9 cm. During the Permian, these simple burrows have a similar morphology and size, with an average diameter of 3–9.5 cm. Some taper distally (Hembree et al., 2004, 2005), some have a flask-shape (Vaughn, 1964). During the Triassic, morphology and size of sub-vertical burrows are still consistent, with an average diameter of 3.8–8.6 cm. These structures are mostly found in mudstone and passively filled in, can occur in high density, and can be associated with pedogenesis and desiccation structures. These can be considered aestivation burrows made by different kind of vertebrates (mostly lungfishes and recumbirostran "microsaurs") (e.g., Greenwood, 1986; Hembree et al., 2004, 2005).

Sub-horizontal potential tetrapod burrows appear in the Carboniferous, have a biconvex section and they already show features such as straight to curved/sinuous tunnels, enlarged chambers and scratch traces. Their average diameter is 8–16 cm and they are found in both mudstone and sandstone. Also, complex burrows are described, but their attribution to either vertebrates or invertebrates is unclear (Hembree et al., 2011).

During the Permian, sub-horizontal tetrapod burrows are similar to those described from the Carboniferous, but helical structures (e.g., Smith, 1987; Martens, 2005) appear for the first time. Other structures that may have appeared at this time are: bottom medial ridges (Buchwitz et al., 2018), complex burrows (Lagnaoui et al., 2015), and dug-out nests (Voigt, 2005). The host rock can be either mudstone or sandstone. Moreover, the average diameter is significantly larger, 9.8–25.6 cm.

During the Early Triassic, the earliest definite complex vertebrate burrows with a medial bottom ridge are described (e.g., Groenewald et al., 2001; Krummeck and Bordy, 2018). Additional features such as distally tapering tunnels (e.g., Groenewald et al., 2001) are observed. Features such as tunnel branching (e.g., Miller et al., 2001) and a medial bottom ridge (e.g., Krummeck and Bordy, 2018) become common. The average diameter is 10.9–26 cm, similar to Permian occurrences. However, these burrows are mostly found in mudstone.

During the Middle Triassic, enlarged chambers become more common, as well as sandstone as the host rock (e.g., Voigt et al., 2011; Bordy et al., 2019). The average diameter is 6.9–14.1 cm, significantly smaller than in the Early Triassic. During the Late Triassic, the features of sub-horizontal burrows are similar, but the average diameter is 9.3–20.7 cm; increased compared to the Middle Triassic. Supposed vertebrate nests are described (Avanzini et al., 2007), although the first fossil nests with egg remains date only to the Early Jurassic (Reisz et al., 2012; Pol et al., 2021).

Therefore, it is clear that the main structural features of sub-horizontal tetrapod burrows appeared in the Carboniferous, additional features appeared in the Permian and the size increased, and in the Triassic a peak in abundance and complexity was reached. The increase in size in the Permian may be related to the acquisition of fossoriality in new tetrapod clades with a larger size range (e.g., Smith et al., 2021).In the Palaeozoic–Triassic record, the average size of sub-horizontal

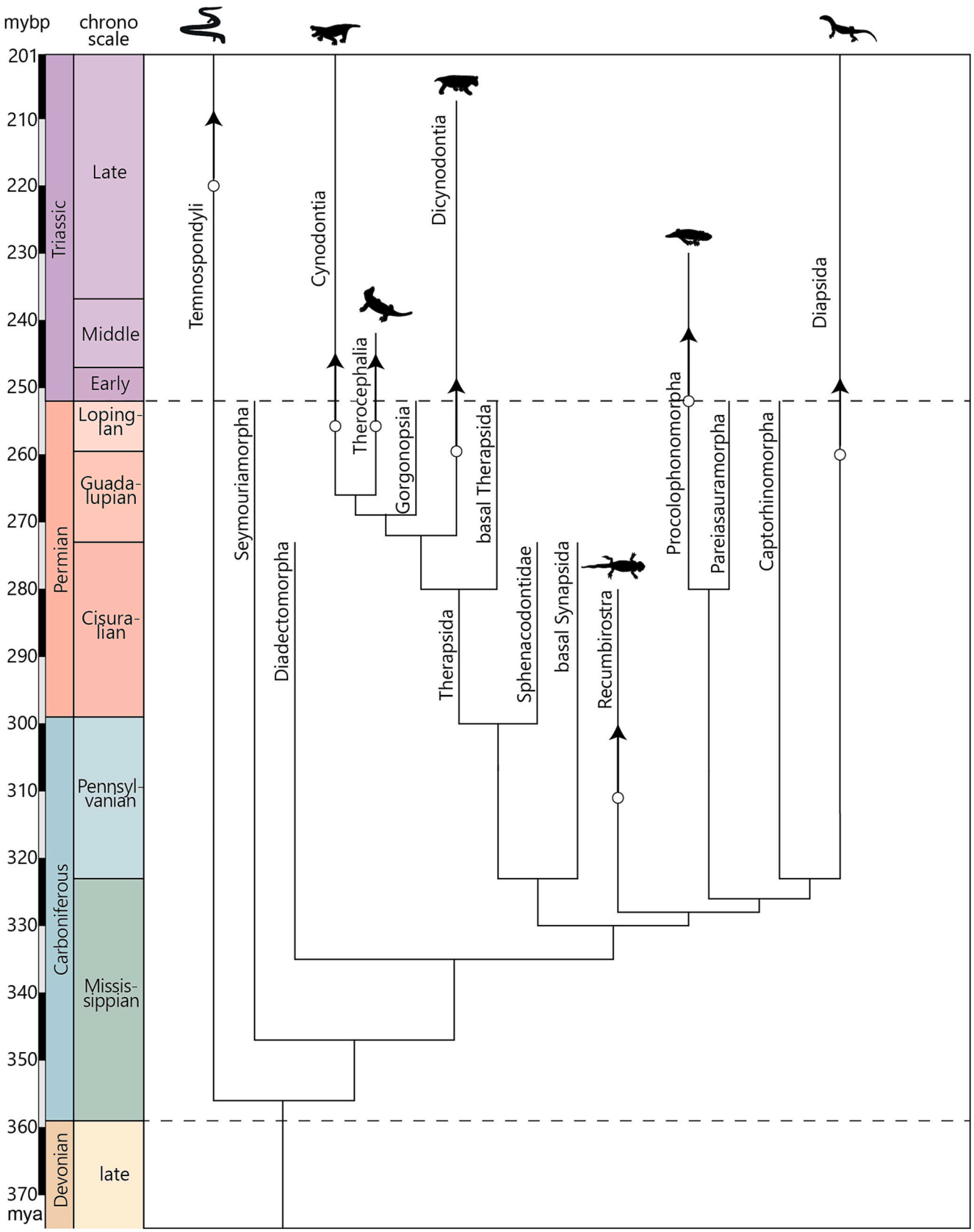

Fig. 15. Simplified phylogeny of Devonian-Triassic fossorial tetrapods, based on Ruta and Coates, 2007), Kemp (2011), Witzmann and Schoch (2018), Pardo et al. (2017) and MacDougall et al. (2018). Empty circles represent the first occurrence of fossoriality in the group.

burrows with bottom ridges is 6.5–14.7 cm, significantly smaller than sub-horizontal biconvex burrows, which are 11.38–25.36 cm in diameter; this is consistent with different producers. The host rock was more commonly sandstone during the Palaeozoic, whereas mudstone initially became more common in the Triassic, especially in the aftermath of the end-Permian extinction, with burrows found in more distal floodplain environments. This may be related to changes in the fluvial regimes and water table that generated drier floodplains more suitable for burrowing (e.g., Smith, 1995). The function of the sub-horizontal burrows could have been aestivation, temporary shelter, dwelling, and breeding, depending on the degree of complexity and the use of the structure by burrower or non-burrower taxa. Producers of these structures include therapsids such as cynodonts and dicynodonts from the Guadalupian onwards. However, the producers of Carboniferous-Cisuralian large, sub-horizontal burrows are still unidentified.

6.2. *Early vertebrate burrower phylogeny and evolution*

Burrowing behaviour and its associated adaptations have evolved independently in several vertebrate groups (Fig. 15; Table 2), with the earliest known examples of the behaviour appearing in lungfish (Horner and Storrs, 2002; Garcia et al., 2006), and then later in various clades of anamniote tetrapods (temnospondyls,possibly aistopods), reptiles (recumbirostrans [possible reptiles; see Mann et al., 2019], procolophonians, diapsids), and synapsids (cynodonts, dicynodonts, therocephalians). Burrowing evolved in all three of these major terrestrial tetrapod groups relatively early in their evolutionary histories, during the late Palaeozoic/early Mesozoic (Fig. 15). This suggests that it was an important adaptation for the survival of many tetrapods during their early evolution, as is the case in the modern world, where fossorial behaviour plays an important role in the life histories of many extant vertebrates (Hildebrand, 1974, 1985; Liow et al., 2009; Riddell et al., 2021). Furthermore, it is also apparent that some anatomical features

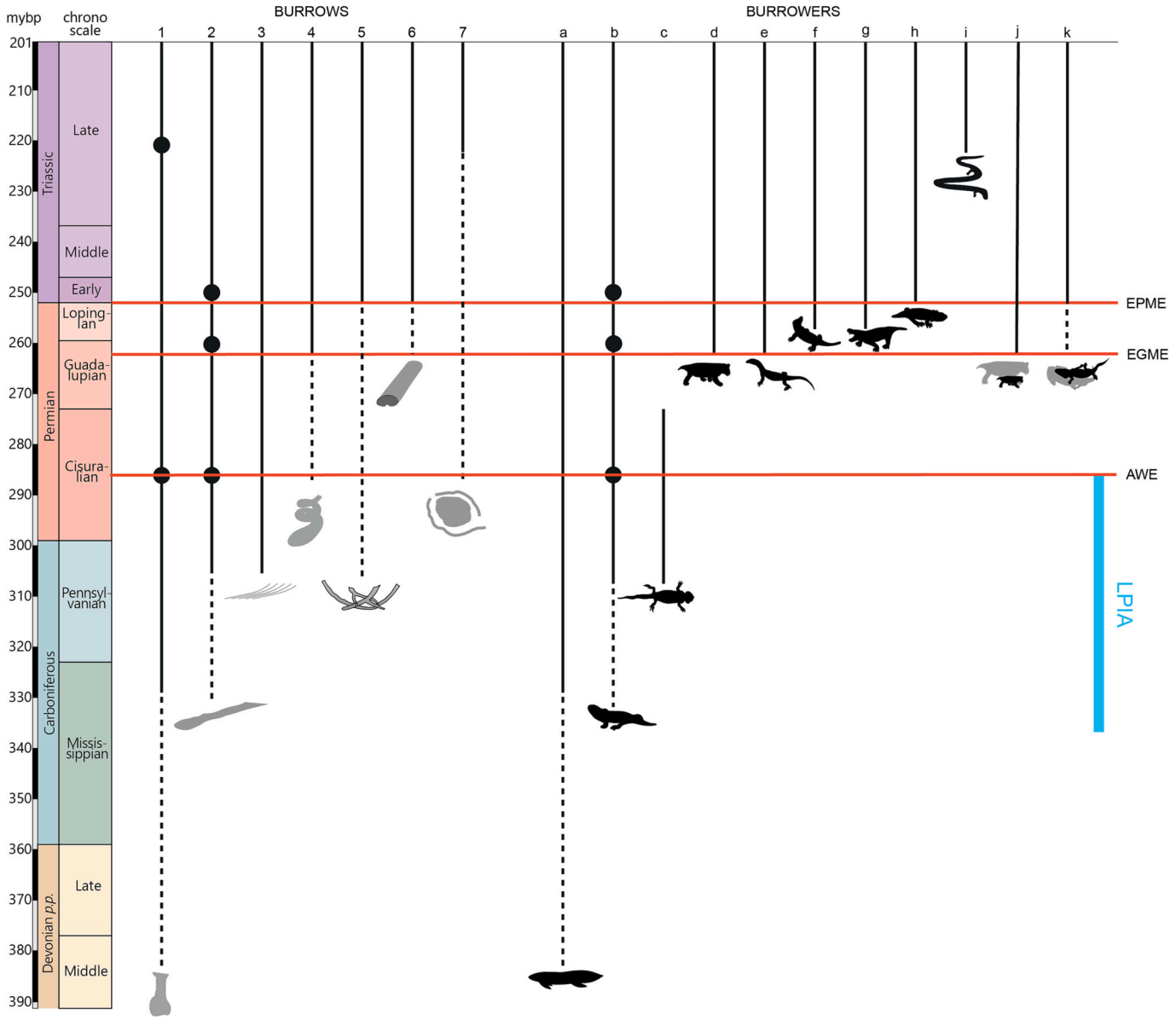

Fig. 16. Key innovations in vertebrate fossoriality from Devonian to Triassic. 1-fish burrows, 2-tetrapod burrows, 3-scratch traces, 4-spiral tunnels, 5-complex burrows, 6-bilobate burrow section, 7-nests. a-fossorial fishes, b-fossorial tetrapods, c-recumbirostrans, d-dicynodonts, e-diapsids, f-cynodonts, g-therocephalians, h-procolophonids, i-temnospondyls, j-juvenile/adult co-occurrence, k-different taxa co-occurrence. LPIA-Late Palaeozoic Ice Age, AWE-Artinskian Warming Event, EGME-end Guadalupian mass extinction, EPME-end-Permian mass extinction. Circles represent increased abundance and diversity.

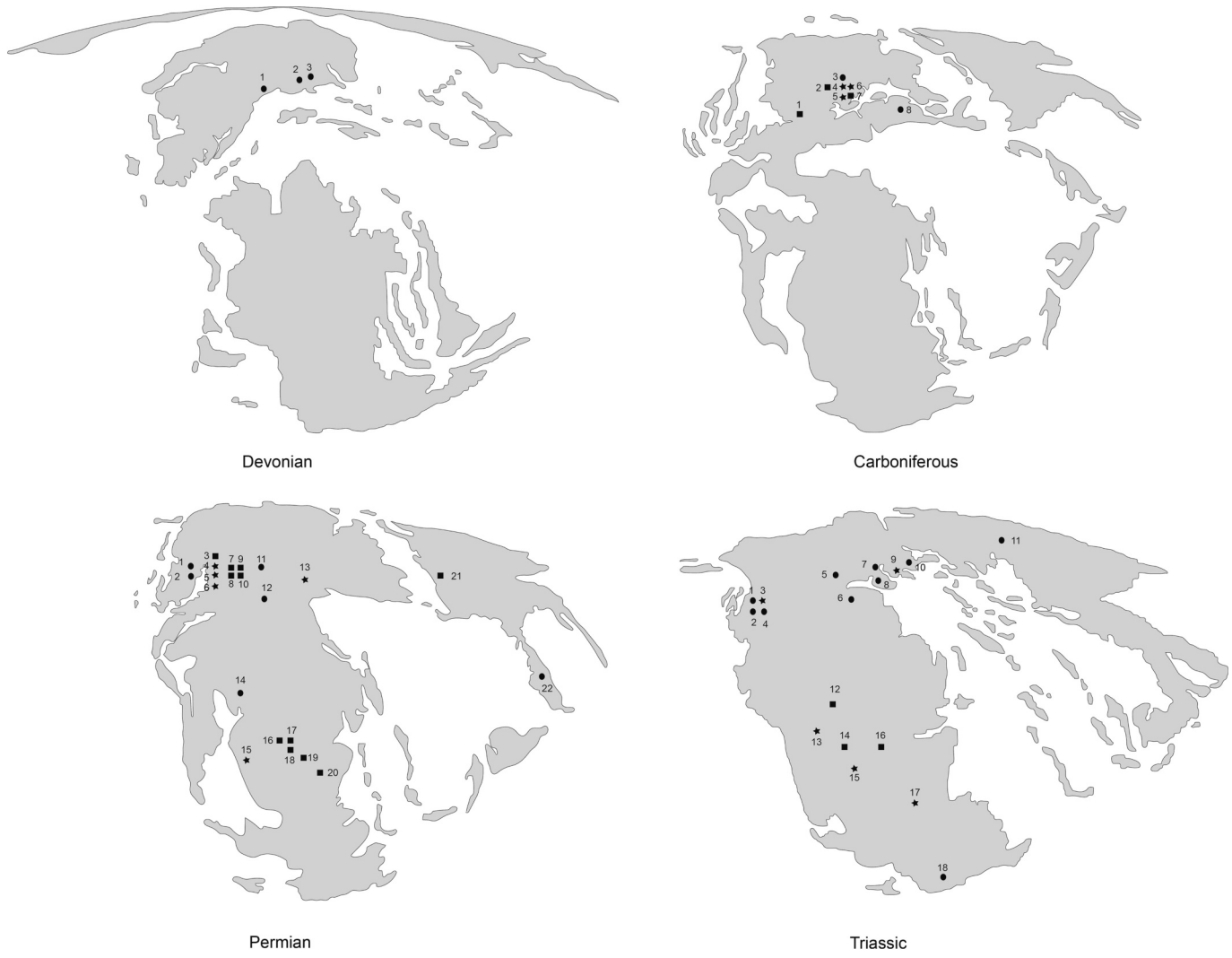

Fig. 17. Palaeogeographic distribution of vertebrate burrows (circles), burrowers (squares), co-occurrence of both (stars). Devonian: 1-Pennsylvania, 2-Ireland, 3-Scotland. Carboniferous: 1-New Mexico, 2-Illinois, 3-Michigan, 4-Ohio, 5-Kentucky, 6-Pennsylvania, 7-West Virginia, 8-Germany. Permian: 1-Colorado, 2-New Mexico, 3-Nebraska, 4-Kansas, 5-Oklahoma, 6-Texas, 7-Ohio, 8-West Virginia, 9-Pennsylvania, 10-Maryland, 11-Prince Edward Island, 12-Morocco, 13-Germany, 14-Brazil, 15-South Africa, 16-Zambia, 17-Tanzania, 18-Malawi, 19-Madagascar, 20-India, 21-Russia, 22-China. Triassic: 1-Utah, 2-Arizona, 3-Colorado, 4-New Mexico, 5-Nova Scotia, 6-Morocco, 7-England, 8-France, 9-Germany, 10-Poland, 11-Russia, 12-Brazil, 13-Argentina, 14-Namibia, 15-South Africa, 16-Zambia, 17-Antarctica, 18-Australia. Palaeogeographic maps redrawn from Blakey (2008).

related to fossoriality have evolved multiple times over the course of early vertebrate evolution, such as the long unguals of some synapsids (Fontanarrosa et al., 2019) and diapsids (Dróżdż, 2018), the elongated bodies of some recumbirostrans (Bolt and Wassersug, 1975) and stem-caecilians (Pardo et al., 2017; Kligman et al., 2023), limb-reduction and loss in recumbirostrans (Mann et al., 2022) and stem-caecilians (Kligman et al., 2023), and similar microstructural adaptations, such as those found in both cynodont synapsids (Botha and Chinsamy, 2004) and procolophonid reptiles (Botha-Brink and Smith, 2012). These similar characteristics convergently arose due to the anatomical and physiological constraints that a fossorial lifestyle would have placed on the bodies of early tetrapods, such as living in confined spaces, the compressive forces exerted on the body, and movement through the surrounding substrate.

6.3. *Palaeoecological inferences using bone microstructure*

Palaeoecological inferences pertaining to the potential fossorial adaptations of numerous Permo-Triassic taxa (mainly therapsids, but also reptiles) have often been substantiated based on bone microstructure. However the relationship between fossorial lifestyle and bone microstructure in extant tetrapods is complex and still incompletely understood. Studies investigating the effects of digging behaviours on bone microanatomy and histology have been carried out on small or taxonomically restricted (mostly mammalian) samples, not encompassing the full phylogenetic breadth of fossorial tetrapods. Furthermore, in large comparative studies, fossorial groups were often treated as a homogeneous ecological category despite the diversity of digging styles, degree of fossoriality, and physiologies encountered in extant digging tetrapods, aspects that could all independently affect the bone microstructure of these animals. Despite these caveats, a high cortical thickness (e.g., Nasterlack et al., 2012; Lyson et al., 2016) or the presence of compacted coarse cancellous bone (e.g., Avrahami et al., 2019) in the mid-diaphysis of limb bones have been considered as indicative of a fossorial lifestyle in palaeoecological reconstructions. However, both characters should be considered carefully. Indeed, comparative studies have consistently emphasized that both fossorial and semi-aquatic tetrapods share a similar microstructural pattern, with more ellipsoid cross-sections and higher cortical thickness than terrestrial or aerial relatives (although the causes and associated modeling processes may be

different). These lifestyle adaptations are thus difficult to discriminate based on cortical thickness and global compactness only (Laurin et al., 2011; Parsi-Pour and Kilbourne, 2020; Amson et al., 2022). Similarly, large amounts of compacted coarse cancellous bone have been reported in the long bone diaphyses of semi-aquatic taxa, such as the beaver (*Castor fiber*; Geiger et al., 2013), the river otter (*Lutra lutra*; Buffrénil et al., 2021), or the king penguin (*Aptenodytes patagonicus*; Canoville and de Buffrénil, 2016). The presence of compacted coarse cancellous bone in these groups could be the outcome of modeling processes leading to cortical thickening through ontogeny, rather than a direct adaptation to fossoriality. Further investigations are thus needed to untangle the effects of semi-aquatic and fossorial adaptations on bone inner structure. Until then, bone microstructure alone should not be considered to draw rigorous palaeoecological inferences related to fossoriality, but should be considered in conjunction with other types of evidence, such as morphological and taphonomical data.

6.4. Early vertebrate burrowing evolution, biogeography, and climate

During the Devonian-Triassic, burrowing in vertebrates underwent some major innovations, fossorial animals radiated, and burrows became more abundant and structurally diverse, which seem to be related to climate change (Fig. 16). Simultaneously, the palaeobiogeographical distribution of fossils testifying to vertebrate fossoriality increased (Fig. 17).

The earliest supposed vertebrate burrows are from the Devonian (Givetian) (Fig. 16), specifically *Cornulatichnus edayensis* Carroll and Trewin, 1995 from Scotland, a cone-like vertical structure potentially produced by an eel-like fish. The oldest potential lungfish burrows are sub-vertical structures described from the Old Red Sandstone of Ireland, and are dated Givetian-Fammenian (O'Sullivan et al., 1986). However, the Devonian vertebrate burrow record is scattered, often confused with invertebrate burrows, and vertebrate skeletal remains have not been found within such burrows to date. The geographic distribution of the potential Devonian vertebrate burrows is restricted to North America and Europe (Fig. 17A).

The earliest find of a lungfish skeleton within a burrow is from the early Carboniferous (Mississippian, Namurian A) Menard Limestone of Kentucky (Horner and Storrs, 2002; Garcia et al., 2006) (Fig. 16). In the early Carboniferous, there is also the first appearance of potential tetrapod burrows, including sinusoidal tunnels and enlarged chambers (late Mississippian Mauch Chunk Formation of Pennsylvania; Storm et al., 2010) (Fig. 16). The appearance of tetrapod fossoriality in the Mississippian is consistent with a regionalization of the axial skeleton and body stem musculature of early tetrapods (e.g., Stewart et al., 2022), which enabled specialized head and limb movements necessary for burrowing.

In the Pennsylvanian (Moscovian), there is the first occurrence and diversification of definite tetrapod burrowers exhibiting fossorial features of the skeleton, i.e., the recumbirostrans from the Francis Creek Shale, Illinois (Mann and Maddin, 2019; Mann et al., 2019, 2021, 2022) (Fig. 16), although Mann et al. (2020) suggest a possible earlier appearance of the group, from the Bashkirian Joggins Formation of Nova Scotia. Shortly before the Carboniferous-Permian transition, subhorizontal burrows with scratch traces testify the earliest documented tetrapod scratch-digging behaviour (Gzhelian Ilmenau Formation of Germany; Voigt, 2005) (Fig. 16). Complex burrows have been described from Pennsylvanian units, but their attribution to either vertebrates or invertebrates is uncertain (Hembree et al., 2011) (Fig. 16). The Pennsylvanian radiation of tetrapod fossoriality may also be the result of innovations such as the amniotic egg, which overcomes dependence on water bodies but requires coverage or burrowing. This is coupled with a reduced number of (more complex) eggs in comparison to bony fish, which may have initiated more cost-intensive nesting behaviour (e.g., Kohring, 1995). Amniotes appeared first in the Early Pennsylvanian (Bashkirian) in both the skeletal and footprint record (e.g., Carroll, 1964; Marchetti et al., 2021). Also, the radiation of non-marine invertebrates in soils and freshwater bodies and the more common presence of soils may have been factors that drove the acquisition of fossoriality in certain tetrapod groups, because of the increase in suitable sediment and food available when burrowing (e.g., Buatois et al., 1998; DiMichele et al., 2009).

The geographic distribution of Carboniferous vertebrate burrows and burrowers is still restricted to North America and Europe (Fig. 17B).

The early Permian is characterised by a worldwide aridification trend, passing from an icehouse to a greenhouse climatic setting (e.g., DiMichele et al., 2006; Montañez et al., 2007). The peak of this transition was in the Artinskian (AWE - Artinskian Warming Event of Marchetti et al., 2022b), when volcanically induced levels of CO_2 in the atmosphere increased, creating a greenhouse effect. The low latitudes became drier and more seasonal, and the Antarctic ice cap melted, signaling the end of the Late Palaeozoic Ice Age (LPIA) (Montañez and Poulsen, 2013) (Fig. 16). This seems to be connected with the vertebrate burrow and burrower fossil record, with fossoriality increasing substantially in this time interval with regards to both diversity and abundance (Fig. 16). In particular, sub-vertical burrows attributed to lungfishes and recumbirostran "microsaurs" become very abundant by the Sakmarian-Artinskian of North America (e.g., Romer and Olson, 1954; Olson and Bolles, 1975; McAllister, 1992; Hembree et al., 2004, 2005) (Fig. 16). Several examples, such as the ichnotaxon *Torridorefugium eskridgensis*, preserve skeletons of the producers in life position, including the lungfish *Gnathorhiza* and the recumbirostran *Brachydectes*. Also, a Sakmarian-Artinskian radiation of recumbirostran "microsaurs" can be observed in North America and Europe (e.g., Bolt and Wassersug, 1975; Anderson et al., 2009; Henrici et al., 2011; Maddin et al., 2011; Huttenlocker et al., 2013; Glienke, 2015; Pardo et al., 2015; Szostakiwskyj et al., 2015; Gee et al., 2019; MacDougall et al., 2021) (Fig. 16). Moreover, large-sized tetrapod burrows with scratch traces are reported from units with a similar age from North America and Europe (e.g., Martens, 2005; Voigt et al., 2021) (Fig. 16). Thus, burrowing became a common behaviour among vertebrates to endure increasingly seasonal and arid climatic conditions, by aestivating or excavating dwelling structures.

The end of the Guadalupian is characterised by a disrupting, climate-driven continental extinction event, shortly before the transition to the Lopingian (e.g., Day et al., 2015). During and shortly after this event, there is the earliest definite occurrence of spiral burrows (Smith, 1987) (Fig. 16), structures that, by comparison with modern taxa, could have a breeding function. Abundant spiral and sub-horizontal tetrapod burrows are described from the lower Teekloof Formation of South Africa (Smith, 1987). Some include the dicynodont therapsid *Diictodon*, and also associated adult and juvenile skeletons, representing the possible earliest evidence of breeding in burrows by tetrapods (Smith et al., 2021) (Fig. 16). Moreover, the oldest supposed fossorial therapsid (*Diictodon*) and diapsid (*Eunotosaurus*) are from the late Guadalupian of South Africa, and they are locally abundant (Ray and Chinsamy, 2004; Lyson et al., 2016). So, the increased burrowing of vertebrates, vertebrate burrowers, and burrowing functions, such as breeding, seem to be coeval with the Guadalupian extinction (Fig. 16). The earliest potential complex tetrapod burrows have been reported from the late Permian of Morocco (Lagnaoui et al., 2015) and the earliest potential burrows with central ridges have been reported from similar-aged deposits in Germany (Buchwitz et al., 2018) (Fig. 16).

Permian vertebrate burrows and burrowers have a global distribution, comprising findings from North America, South America, Africa, India, Europe, Russia, and China (Fig. 17C). Notably, this global distribution is achieved by the Guadalupian. This wide area encompasses localities from equatorial to mid-high latitudes. It is unclear whether the significantly smaller Devonian-Cisuralian distribution is a research bias, a taphonomic bias, if it represents the actual distribution, or if it is a combination of multiple factors. Nevertheless, it is remarkable how the structural burrow complexity, ethological function, and burrower

diversity was already high before the end-Permian mass extinction, unlike what has previously been hypothesized (e.g., Hasiotis et al., 2007).

The transition between the Permian and Triassic is characterised by the largest extinction event in the history of Earth, the effects of which are also registered in continental settings, between the *Daptocephalus* and *Lystrosaurus declivis* AZs in South Africa (e.g., Benton and Twitchett, 2003; Viglietti et al., 2021). The aftermath of this extinction is characterised by abundant and diverse tetrapod burrows and burrowers in South African, Antarctic, and Australian localities (e.g., Groenewald et al., 2001; Miller et al., 2001; Damiani et al., 2003; Bordy et al., 2011; Botha-Brink, 2017; Krummeck and Bordy, 2018; McLoughlin et al., 2020) (Fig. 16). These include the earliest definite complex tetrapod burrows, from the Burgersdorp Formation of South Africa (Groenewald et al., 2001), which can be considered dwelling structures. Neurological changes that enable herd behaviour/group behaviour may have been developed at that time, which in turn is a prerequisite for communal burrowing (e.g., Williamson et al., 2016).

The earliest described burrows with a kidney-shaped section, *Reniformichnus* (Krummeck and Bordy, 2018; McLoughlin et al., 2020) (Fig. 16), are interpreted as an effect of a more erect posture of the producers, likely cynodont therapsids (Damiani et al., 2003). Furthermore, there is the earliest definite co-occupation of burrows by different clades, from the Normandien Formation of South Africa (Fernandez et al., 2013) (Fig. 16). This includes the probable burrow producer, the cynodont *Thrinaxodon liorhinus*, and the temnospondyl *Broomistega putterilli*, which may have occupied the burrow for shelter after injury. This co-occurrence may represent the earliest occurrence of ecosystem engineering in burrowing vertebrates. Other skeletons found in burrows in this time interval belong to the dicynodont *Lystrosaurus curvatus* and the cynodonts *Thrinaxodon* and *Langbergia* (Groenewald et al., 2001; Damiani et al., 2003; Abdala et al., 2006a, 2006b; Botha-Brink, 2017). Both *Lystrosaurus* and *Thrinaxodon* are common taxa in the *Lystrosaurus declivis* AZ (Viglietti et al., 2021), with *Langbergia* occurring in the lowermost part of the overlying *Cynognathus* AZ (Hancox et al., 2020). In addition, the earliest "parareptilian" fossorial taxa appear in the Early Triassic fossil record (e.g., Botha-Brink and Smith, 2012) (Fig. 16). In summary, the end-Permian mass extinction was followed by a substantial increase in tetrapod burrow abundance, diversity, complexity, ethological function, and by an increase of potential tetrapod burrowing taxa.

In some instances, burrowing can be viewed as a potential survivor's gate through a mass extinction (e.g., Wolvaardt et al., 2023). Burrowing in temnospondyls and "parareptiles" has been stated to occur in the Triassic, but morphological adaptations for it already occur in late Palaeozoic taxa and might have played a role in the survival of these groups through the end-Permian extinction event (e.g., Botha-Brink and Smith, 2012).

The Triassic is generally considered to have had a hothouse climate, which is consistent with the vertebrate burrow record (e.g., Joachimski et al., 2022). The Middle and Late Triassic are characterised by relatively widespread complex tetrapod burrow systems, described from South Africa, Morocco, South and North America (e.g., Voigt et al., 2011; Colombi et al., 2012; Fiorelli et al., 2018; Bordy et al., 2019). Therefore, it is probable that burrowing in tetrapods became related to permanent or long-term dwelling to seek better temperature and humidity conditions than at the surface, for instance a cooler and more humid environment during times of prevailing hot, dry climate. Wolvaardt et al. (2023) reported on the presence of small-bodied terrestrial tetrapods in association with tetrapod burrow casts of compatible size in an Early-Middle Triassic Karoo locality indicating an apparent Lilliput effect. It is suggested that this Lilliput effect is due to the preadapted or acquired burrowing behaviour of small-bodied terrestrial animals after the end-Permian extinction event that led to increased survivorship in a harsh environment where large animals were not able to cope.

In the Late Triassic, an increase in vertical aestivation burrows attributed to lungfish in North America, such as *Redondarefugium abercrombieorum*, is observed (Lucas et al., 2010). Also, the earliest temnospondyl burrowers are described (*Chinlestegophis* Pardo et al., 2017 and *Funcusvermis* Kligman et al., 2023) (Fig. 16). While the geologically older temnospondyl *Broomistega* was found in a burrow, its skeletal morphology is not compatible with burrowing behaviour. From the Late Triassic, there are also the earliest structures firmly interpreted as tetrapod nests (e.g., Hasiotis et al., 2004; Avanzini et al., 2007) (Fig. 16).

Triassic vertebrate burrows and burrowers have a global distribution, enclosing findings from North and South America, Europe, Russia, Africa, Australia, and Antarctica (Fig. 17D). This, together with the noteworthy structural complexity, diversity of ethological function, and diversity of producers, seem to support the definite role of burrowing as widespread behaviour in continental environments during the Triassic.

7. Conclusions and perspectives

This first comprehensive review on the origin and evolution of fossoriality in vertebrates, with modern-day fossoriality as comparison, indicates:

- a probable Devonian earliest occurrence of vertebrate fossoriality;
- a Carboniferous earliest occurrence of tetrapod fossoriality;
- a Permian acquisition of fossoriality in several distantly-related vertebrate clades;
- a Permian diversification and increase in size of burrowing structures;
- a Permian earliest occurrence of parental care associated with burrows and possibly nests;
- a Triassic definitive establishment of vertebrate burrowing with clear dwelling/communal structures, possible ecosystem engineering, and a broad burrow diversity and producer diversity;
- a clear increase in fossoriality during important faunal events such as the end of the LPIA, the AWE, and the end-Guadalupian and end-Permian mass extinctions from a qualitative analysis;
- an increase of burrows in distal floodplains in the aftermath of the end-Permian mass extinction, probably linked to a change of fluvial regimes;
- burrowing behaviour provided a mechanism for tetrapods to cope with harsh environmental conditions during and after mass extinction events;
- the importance of understanding the taphonomy of fossil vertebrate burrows and the taphonomy of bone remains found in burrow infills;
- the necessity of a more comprehensive ichnotaxonomy of vertebrate burrows, presently regarding mostly simple structures;
- the necessity of a multi-disciplinary approach to infer the burrow producers and fossoriality in extinct taxa;
- the potential of the study of bone macro- and micro-structures in comparison with the modern record to infer vertebrate fossoriality.

This study showed that the origin and early evolution of vertebrate fossoriality is far from being completely explored and understood. While some results, such as the earliest occurrence of vertebrate and tetrapod burrows, are consistent with previous studies, some such as the Permian diversity of burrows and burrowers and the increase of fossorial evidence in the frame of three different climatic crises were unexpected. Further studies should clarify taphonomy, ichnotaxonomy, taxonomic affinity to fossoriality, and clearly define the earliest occurrences of key behaviours associated to fossoriality such as parental care, communal behaviour, and ecosystem engineering, especially in the frame of key faunal events/crises in the Devonian-Triassic.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No new data was produced for the research described in the article.

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